

SOCIAL BEHAVIOR OF NORTH AMERICAN TIDAL-MARSH VERTEBRATES

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Abstract. We examine the relationship between the social behavior of terrestrial vertebrates and the unique biophysical characteristics of tidal marshes with emphasis on birds, particularly those species and subspecies restricted to tidal marshes. However, where relevant, examples from mammals are also included. Tidal marshes are structurally and floristically simple habitats that are highly productive and spatially variable in quality, a variability that is magnified by the local effects of tidal inundation. Such conditions are thought to contribute to the evolution of polygynous mating systems. Over half (five species) of the saltmarsh-breeding species are commonly polygynous. This distribution of mating systems is not appreciably different from closely related species or subspecies of freshwater marsh or grassland habitats. The distribution of breeding territories in some tidal-marsh birds show a strong tendency to aggregate around certain habitat features, leaving regularly flooded tidal flats as shared feeding areas. In addition, some mammals show a tendency to form aggregations and an increase in social tolerance, partly in response to the forced crowding the tidal flooding can impose. The unusual non-territorial spacing behavior and related scramble, polygynous mating system of the sharp-tailed sparrows (*Ammodramus* spp.) may be an endpoint in the tendency for sparrows to occur in local high-density semi-colonial conditions, where males are no longer to defend territories. The sharp-tailed sparrow social system may have evolved in response to its subordinate relationship with syntopic Seaside Sparrows (*Ammodramus maritimus*). In this structurally simple, but zonal habitat, interspecific territoriality and avoidance seem to be well developed among passerine and possibly small mammal taxa.

Key Words: *Ammodramus*, bird, breeding patterns, mammal, mating systems, salt marsh, spatial distributions.

COMPORTAMIENTO SOCIAL DE VERTEBRADOS DE MARISMA DE MAREA NORTE AMERICANOS

Resumen. Examinamos la relación entre el comportamiento social de vertebrados terrestres y las características biofísicas únicas de marismas de marea, haciendo énfasis en aves, particularmente aquellas especies y subespecies restringidas a marismas de marea. Sin embargo, donde era relevante, también fueron incluidos ejemplos de mamíferos. Los marismas de marea son habitats simples estructural y florísticamente, los cuales son altamente productivos y espacialmente variables en cualidad, una variabilidad que es magnificada por los efectos locales de inundaciones de marea. Dichas condiciones, se piensa que contribuyen a la evolución de sistemas de apareamiento poliginuos. Por encima (cinco especies) las especies reproductoras de marisma salada son poliginuas. Esta distribución de sistemas de apareamiento no es apreciablemente diferente de especies o subespecies cercanamente relacionadas de marisma de agua fresca o habitats de pastizal. La distribución de territorios de reproducción en algunas aves de marisma de marea, muestran una fuerte tendencia a acumular ciertas características alrededor de su hábitat, dejando por lo regular las planicies inundadas por marea como áreas de alimentación compartidas. Además, algunos mamíferos muestran una tendencia a formar agrupaciones y un incremento en la tolerancia social, en parte en respuesta al amontonamiento forzado que impone la inundación de marea. El comportamiento espacial no territorial inusual y la lucha relacionada, sistema poligineo de apareamiento de los gorriones cola aguda quizás sean un punto final en la tendencia en los gorriones que acontece en condiciones de densidad local-alta y semi-colonial, en donde los machos ya no defienden el territorio. El sistema social del gorrión cola aguda quizás haya evolucionado en respuesta a su relación subordinada con gorriones costeros sinotópicos (*Ammodramus maritimus*). En este estructuralmente simple, pero hábitat de zona, territorialidad interespecífica y evitación parecen estar bien desarrolladas entre los colorines y posiblemente en taxa mamífera pequeña.

Studies of the social behavior of marsh birds over the past 40 yr have formed the basis of theories for the evolution of territorial polygyny (Verner and Willson 1966, Orians 1969; Searcy and Yasukawa 1989, 1995), coloniality (Orians and Christman 1968) and

interspecific territoriality (Orians and Willson 1964; Murray 1971, 1981). However, most of this research has focused on bird populations in freshwater marshes, and the biophysical environment of tidal marshes is quite distinct from interior marshes in ways that might

further influence the evolution of social behavior. Social systems have been investigated in a few tidal-marsh species, most notably species in the genus *Ammodramus* (Post and Greenlaw 1982, Greenlaw and Post 1985). To date, no comprehensive overview of social systems of tidal-marsh birds has been published. This paper will provide such an overview from a behavioral ecology and evolutionary point of view, wherein we pose two questions: What is the nature and extent of variation of the social behavior observed in tidal salt marsh animals? What saltmarsh environmental features may lead to favoring or disfavoring certain social strategies?

METHODS

Because most detailed behavioral studies of tidal-marsh vertebrates have been directed at birds, particularly passerines, this paper will have a strong avian focus. However, some important observations have been made on other vertebrates, particularly small mammals, and these will be discussed as well.

The analyses in this paper are based on the descriptions and classifications of social behavior for North American saltmarsh birds based on the literature. Bird species are classified by migratory status, breeding territorial system, patchiness of distribution, and mating system in Tables 1 and 2; they are divided between saltmarsh species (Table 1) and saltmarsh relatives

(Table 2). We believe the more scant information on mammalian social systems would not support such a classification scheme, but we have incorporated examples from small-mammal studies in the body of the paper.

KEY CHARACTERISTICS OF TIDAL MARSHES

Saltmarshes, as contrasted to inland habitats, have four key attributes which might shape the evolution and expression of social behavior: (1) higher food abundance, particularly for species dependent upon invertebrates, (2) lower seasonality in resource abundance, (3) lower structural and floristic diversity, and (4) habitat quality variability dependent on patterns of tidal flooding, which in turn influences vegetation cover.

HIGH FOOD ABUNDANCE

Tidal marshes are known for their high primary productivity (Adam 1990), which should ultimately lead to high food abundance for herbivores, detritivores, and their predators. Post and Greenlaw (1982) hypothesized that food is rarely, if ever, a limiting factor shaping the population dynamics or social systems of tidal-marsh birds, at least during the breeding season. By this hypothesis, individuals should not be expected to adopt a strategy that provides greater access to food because increasing

TABLE 1. BREEDING SOCIAL SYSTEM ATTRIBUTES OF NORTH AMERICAN TIDAL-MARSH BIRDS.

Species	Migratory status ^a	Territorial system ^b	Patchiness ^c	Mating system ^d	References
Clapper Rail (<i>Rallus longirostris</i>)	R-M	2	P	M	Eddleman and Conway (1998).
Willet (<i>Catoptrophus semipalmatus</i>)	M	2		M	Howe (1982).
Marsh Wren (<i>Cistothorus palustris</i>)	R-M	1	P	P	Kale (1965).
Common Yellowthroat (<i>Geothlypis trichas</i>)	R-M	1		M	Foster (1977).
Song Sparrow (<i>Melospiza melodia</i>)	R	2	P	M	Johnston (1956a, b).
Swamp Sparrow (<i>Melospiza georgiana</i>)	M	1	P	M	Greenberg and Droege (1990).
Seaside Sparrow (<i>Ammodramus maritimus</i>)	R-M	2	P	M	Post and Greenlaw (1994).
Nelson's Sharp-tailed Sparrow (<i>Ammodramus nelsoni</i>)	M	3	P	P	Shriver (2002).
Salt Marsh Sharp-tailed Sparrow (<i>Ammodramus caudacatus</i>)	M	3	P	P	Greenlaw (1993).
Savannah Sparrow (<i>Passerculus sandwichensis</i>)	R	1?		M	Powell and Collier (1998), J. Williams (pers. comm.).
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	R-M	2	P	P	Reinert (<i>this volume</i>).
Boat-tailed Grackle (<i>Quiscalus major</i>)	R-M	3	P	P	Post et al. (1996).

^a Migratory status (M = migrant, R = resident, and R-M = partial migrant).

^b Breeding territorial system (1 = all-purpose territory, 2 = nesting territory with discontinuous supplementary feeding areas, and 3 = non-territorial).

^c Patchy distribution (P = high clumped).

^d Mating system (M = monogamous, P = polygynous).

TABLE 2. BREEDING SOCIAL SYSTEMS OF NON-TIDAL MARSH-RELATIVES OF NORTH AMERICAN TIDAL-MARSH SPECIES.

Species	Migratory status ^a	Territorial system ^b	Patchiness ^c	Mating system ^d	References
King Rail (<i>Rallus elegans</i>)	R-M	1	?	M	Meanley (1992).
Willet (<i>Catoptrophus semipalmatus</i>)	M	1		M	Lowther et al. (2001).
Marsh Wren (<i>Cistothorus palustris</i>)	R-M	1	P	P	Kroodsma and Verner (1997).
Common Yellowthroat (<i>Geothlypis trichas</i>)	R-M	1		M	Guzy and Ritchison (1999).
Song Sparrow (<i>Melospiza melodia</i>)	R-M	1		M	Arcese et al. (2002).
Swamp Sparrow (<i>Melospiza georgiana</i>)	M	1	P	M	McDonald (pers. obs.).
LeConte's Sparrow (<i>Ammodramus leconteii</i>)	M	1	P	M	Murray (1969), Lowther (1996).
Nelson's Sharp-tailed Sparrow (<i>Ammodramus nelsoni</i>)	M	3	P	P	Murray (1969).
Savannah Sparrow (<i>Passerculus sandwichensis</i>)	R-M	1		M/P	Wheelright and Rising (1993).
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	M	2	P	P	Yasukawa and Searcy (1995).
Boat-tailed Grackle (<i>Quiscalus major</i>)	R-M	3	P	P	Post et al. (1996).

^a Migratory status (M = migrant, R = resident, and R-M = partial migrant).

^b Breeding territorial system (1 = all-purpose territory, 2 = nesting territory with discontinuous supplementary feeding areas, and 3 = non-territorial).

^c Patchy distribution (P = high clumped).

^d Mating system (M = monogamous, P = polygynous).

access to food, as opposed to other resources, such as safe nesting sites, will have a negligible effect on reproductive output. Food availability has rarely been quantified, and as far we know food abundance has not been experimentally manipulated to test its importance as a factor in strategies of tidal-marsh birds. Furthermore, assessment of food abundance has to factor in prey quality related to such things as size, distribution, digestibility and salt content of prey items. Post et al. (1982) present some circumstantial evidence that supports the food non-limitation hypothesis. The evidence is three-fold: (1) based on diet analysis and arthropod sampling, prey items used by sparrows are in ample supply, (2) for their focal species (Seaside Sparrow [*Ammodramus maritimus*] and sharp-tailed sparrows), male provisioning is either non-existent (sharp-tailed sparrows) or not necessary when experimentally eliminated (Seaside Sparrow), (3) the focal species have similar diets which appear to be broad and change opportunistically with little selection for diet specialization. Although each of these lines of evidence has merit, the assertion that food is not a critical resource for tidal marsh birds has not been critically tested at a general level.

LOW SEASONALITY

Because of their coastal locality, tidal marshes tend to have a less seasonal climate than interior marshes, grasslands, and other similar habitats. Furthermore, much of the productivity is based on inputs from marine systems, which

also show reduced seasonality in productivity compared to temperate terrestrial habitats. Although the phenology of food resources per se for birds and mammals have not been monitored on an annual basis, it would be reasonable to hypothesize that seasonality of resources is reduced which might have a number of indirect effects on social systems, e.g., longer breeding seasons and increased residency.

STRUCTURAL AND FLORISTIC SIMPLICITY

Being flat, wet, and open grassland areas, tidal marshes share features known to influence social behavior in similar ecosystems such as fresh-water marshes, grassland, and tundra. However, the appearance of homogeneity and low variation in vegetation form may be biased by a human perspective; to a tidal-marsh bird or mammal, great variation may exist for what humans may perceive as only subtle nuances in microhabitat. For example, clumps of grass, such as a rush (*Juncus*) tussock, slightly elevated and/or separated from the other vegetation serve as song posts advantageous in defining defending critical territorial boundaries (McDonald 1986).

SALINITY AS A PHYSIOLOGICAL BARRIER

The effect of salinity on social behavior is probably manifested primarily through the effect that it has on habitat structure and floristic diversity. Salinity may favor certain plants, such as pickleweed (*Salicornia virginia*; Padgett-Flohr

and Isakson 2003) and affect the stature of such plants (see Geissel et al. 1988 for *Salicornia*). Saltmarshes tend to be simple in structure and plant species composition even compared to other wetlands habitats (Mitsch and Gooselink 2000). Because salinity may provide a physiological barrier to potential colonizing species, it is likely that it contributes to the low-species diversity of vertebrates in tidal marshes. Low diversity combined with abundant food resource often leads to high densities of a few dominant species, which is a dominant force shaping the social environment for tidal marsh species.

PATCHY HABITAT QUALITY

Tidal marshes are generally zonal (Mitsch and Gosselink 2000) in their vegetation patterns. Because tidal marshes are dominated by one or a few species, zonal shifts in these dominants may create a pervasive change in habitat quality, such as a shift from pickerelweed to cordgrass (*Spartina*) cover. Within these zonal patterns, small topographic variation may have a large impact on the availability of food, cover, and the propensity of areas to be flooded by regular tides and stochastic flooding. Stochastic flooding of tidal marshes, caused by the combination of wind, rain, and tidal influx, is frequent and sometimes destructive enough to expect that some behavioral adaptations have evolved. One adaptation would be the ability to deal with temporarily crowding with minimal stress and energy expenditure. At a longer time scale, individuals may select areas to nest that have a lower probability of inundation for the reproductive period.

Tidal sloughs, serving as conduits for water and its payload of nutrients and flora, are typically part of the natural tidal-marsh landscape. In some marshes, artificial channels or ditches are present in addition to or instead of natural water channels. Daily or twice-daily tides bring marine waters, which can be advantageous (e.g., replenishing water-associated food sources for prey species, such as crabs [*Uca* spp.], and providing escape from predators for swimming and diving small mammals) or detrimental, e.g., bringing aquatic predators closer to nests. Tidal sloughs may also act as landmarks for territorial and home-range boundaries.

RESULTS

MATE SELECTION AND MATING PATTERNS

Less than half (five of 11) of the saltmarsh species (Table 1), and a similar portion of their non-saltmarsh relatives (four-five of 11) are

polygynous (Table 2). These values are based on a behavioral assessment of mating systems, rather than one based on genetic paternity. We know of a single published study of the frequency of extra-pair paternity in a salt-marsh passerine (Seaside Sparrow; Hill and Post 2005).

The Red-winged Blackbird (*Agelaius phoeniceus*), Marsh Wren (*Cistothorus palustris*) Boat-tailed Grackle (*Quiscalus major*), and two species of sharp-tailed sparrows (Saltmarsh Sharp-tailed Sparrow [*Ammodramus caudacutus*] and Nelson's Sharp-tailed Sparrow [*A. nelsoni*]) have mating systems that differ from monogamy. The first two species commonly display territorial polygyny with two or more females nesting on the territory of some males. The percentage of male Marsh Wrens attracting greater than one female, however, was relatively low in the one tidal-marsh population studied. Kale (1965) found only 5% of males had more than one mate compared to 12–50% in non-tidal marshes (Kroodsma and Verner 1997). Reinert (*this volume*) found that tidal-marsh Red-winged Blackbirds had a small average harem size (1.3) compared to most inland populations studied. He attributes the reduced harem size in saltmarsh populations on the need for males to assist in feeding young to shorten the nesting cycle in the face of tidal flooding.

Sharp-tailed sparrows of both species have truly unusual mating systems for temperate-zone passerines. The Saltmarsh Sharp-tailed Sparrow's system is aptly described as a form of scramble competition polygyny (Post and Greenlaw 1982). In this system, males survey successive areas from exposed perches as they actively roam their home ranges where females are likely to be found and attempt to intercept and copulate with them, usually through forced mating. One to several males may converge on a single female at the same time, or several solitary males may successively interact with a female during a short period. The mating system of the Nelson's Sharp-tailed Sparrow differs from that of the Saltmarsh Sharp-tailed Sparrow in the greater importance of male-male dominance interactions in determining mating success. A small proportion of males may perform a disproportionate share of copulations (Gilbert 1981, Greenlaw and Rising 1994). A dominant male may fight with and chase away other males when a female is present, and then follow her (Greenlaw and Rising 1994).

Due to the importance of direct male-male competition in sharp-tailed sparrows, it might be hypothesized that size dimorphism is greater than in related monogamous species, a divergence driven by the importance of dominance in male-male interactions. However, based

on measurements presented in the literature (Post and Greenlaw 1994, Greenlaw and Rising 1994), this does not seem to be the case for *Ammodramus* sparrows. The potentially heightened importance of sperm competition between males in this species (Greenlaw and Rising 1994) compared to monogamous species might affect patterns of sperm production. In this case, cloacal protuberances in males of some polygynous or promiscuous avian species, such as the sharp-tailed sparrows are unusually large relative to their overall body size. The monogamous Seaside Sparrow, which is substantially larger than sharp-tailed sparrows overall, has a smaller protuberance (Greenlaw and Rising 1994). This intriguing difference between the species needs further exploration with more data on cloacal protuberance but does suggest an important line of comparative research.

Boat-tailed Grackles also displays an unusual mating system for a temperate zone songbird (Post 1992, Post et al. 1996), showing similarities to the sharp-tailed sparrow systems. Males establish dominance hierarchies in the non-breeding season, usually away from colony sites. Females nest in dense colonies in marsh islands or isolated trees, which then attract numerous males. The male's mating success is determined by a strong dominance hierarchy where an alpha male (the identity of whom is often very stable from season to season) garners a plurality ($\approx 25\%$) of the successful mating attempts. As in the sharp-tailed sparrows, males do not defend a territory but compete directly for females.

These few exceptions aside, social monogamy prevails among tidal-marsh species and subspecies. For some bird species monogamy seems to be obligatory, because both sexes are needed to complete incubation (e.g., Clapper Rails [*Rallus longirostris*]; Oney 1954, Eddleman and Conway 1998). In other species, some underlying plasticity is suggested by a small percentage of males have more than one female nesting on their territory. A low frequency of polygyny ($<2\%$) has been reported for tidal-marsh Swamp Sparrow (*Melospiza georgiana*) and Song Sparrow (*M. melodia*; L. J. Grenier, J. C. Nordby, and H. Spautz, pers. comm.), a value which is typical for many temperate zone songbirds. Even in the Seaside Sparrow in which polygyny has never been recorded under natural circumstances, males have been induced experimentally (by removing males during the eggs stage or by using testosterone implants) to accept more than one mate (Greenlaw and Post 1985, McDonald 1986, respectively).

Hypotheses on evolution of monogamy in Seaside Sparrow were tested by Greenlaw

and Post (1985), integrating male-removal experiments, measurements of territory quality, nesting data, and behavioral observations. Experimentally induced bigamy (using hormone implants) in New York (Greenlaw and Post 1985) and Florida (McDonald 1986) indicate that male Seaside Sparrow will accept second mates. Post and Greenlaw concluded that male help is advantageous but not necessary for female reproductive success, and that female-female aggression in Seaside Sparrows is probably not important in maintaining monogamy. Although territory quality was highly variable in the New York Seaside Sparrow populations studied, a polygyny threshold evidently was not exceeded. The authors suggest this was because either resources (food and nest sites) were not limiting, or because females could compensate for the effects of resource food inequality among territories by feeding at distant sites with impunity outside their mates' territories. It is interesting that Hill and Post (2005) report that extra-pair paternity in a locally dense population of Seaside Sparrows was quite low (11% of nestlings) compared to other emberizids. They argue that this is mediated by a high degree of female aggression toward territorial intrusions of non-mate males, and females apparently do not accept extra-pair copulations in shared feeding areas. This suggests that females may need the help of committed mates, after all. A moderately low value of extra-pair paternity (18%) was found in a dense population of San Pablo Song Sparrows (*Melospiza melodia samuelis*; L. Grenier, pers. comm.).

Ratios of mated to unmated birds vary with habitat quality even in the monogamous Seaside Sparrow. For example, in dense breeding populations of New York living in unaltered and hence presumably higher quality marshes, a significantly higher proportion of males were mated, as compared to an artificially ditched marsh (poorer quality) with a low sparrow density. Similarly, at a well-studied Florida Gulf Coast site, the proportion of unmated male Seaside Sparrows varied in frequency, comprising about 10–25% of the territorial males in different parts of study area in the years 1980–1987 (Greenlaw and Post 1985; McDonald 1986, pers. obs.). Again, variation in incidence of unmated males between populations was attributed to habitat suitability (Post et al. 1983, Greenlaw and Post 1985, Post and Greenlaw 1994).

Maintenance and duration of pair bonds

The rate of selecting the same mate in subsequent years can only be approximated for most species, and little is known of winter social

structure of tidal-marsh sparrows. West Coast subspecies are non-migratory, as are Clapper Rail and Seaside Sparrows in the Southeast. In Seaside Sparrows, females of migratory populations returning in spring may or may not mate with their previous mate, perhaps depending on nest-site quality of male territories which varies annually (Post 1974, Post and Greenlaw 1994). In non-migratory populations of Seaside Sparrows, the pair bond appears to be maintained through the year, because both former pair members stay in or around male's former breeding territory (McDonald, pers. obs.; Post and Greenlaw 1994). Similarly, Johnston (1956b) found that resident adult Song Sparrows maintained a non-breeding home range in the vicinity of their breeding territory and these birds were joined in the winter by one or two immatures.

PARENTAL CARE

Animals in resource-rich environments such as tidal saltmarshes should have lessened energetic demands on parents allowing more flexibility in social systems and more instances of single-parent responsibility for the nesting, brooding, and caring for fledged young. With food plentiful, other resource competitions shift to higher prominence. Nest sites and mates are more in demand, and male participation in feeding young may not be as vital in tidal-marsh birds as in non-marsh counterparts. However, complete male emancipation from care of eggs and young has only been found in the sharp-tailed sparrows and Boat-tailed Grackle. Bi-parental incubation occurs in tidal-marsh rails, and biparental feeding of young is found in all species of passerines except the sharp-tailed sparrows, Boat-tailed Grackles, and some Red-winged Blackbirds.

SPATIAL ASPECTS OF TIDAL-MARSH POPULATIONS

Territory clumping and social aggregations

With the exception of male sharp-tailed sparrows, all tidal-saltmarsh birds are territorial during the nesting season. Seven of 11 species or populations diverge from classic all-purpose breeding territories in ways we will discuss below (Table 1). Only three of 11 of the non-saltmarsh populations show such divergence (Table 2).

As with other wetland systems, territory size and density vary considerably, even within a single population. In general, tidal-marsh birds are known for achieving some remarkably high densities with commensurately small

territories. For example, Marsh Wren, aggressively defend territories from 60 to >10,000 m² (Kroodsma and Verner 1997). Territory size for the saltmarsh population in Georgia studied by Kale (1965) was on the small end of this range, averaging approximately 60-100 m² depending upon year and site.

A high proportion of saltmarsh-breeding species (eight of 11) are reported to show highly patchy distribution during the breeding season; this proportion is six of 11 for the non-saltmarsh relatives. A high abundance of food combined with patchily distributed areas safe from predation and flooding might lead to aggregations of high-density nesting territories and sometimes a separation of nesting territories from feeding areas. For example, Johnston (1956b) reports that if the entire tidal marsh was considered potential habitat, then the average density of Song Sparrows would be approximately 2.5 pairs/ha⁻¹. This value however, does not take into account that the actual defended area by breeding Song Sparrows was restricted to the taller vegetation along tidal sloughs. Johnston estimated territory density at approximately 20-25 pairs ha⁻¹. Seaside Sparrows are also noted for their local dense clustering of territories (Post 1974). In northern populations territory size can range from approximately 20 to >10,000 m² in a single marsh.

Territory size varies consistently according to location within the range of the species. Territory size in northern populations of Seaside Sparrows are small compared to southern populations (Post et al. 1983) and, conversely, in the sharp-tailed sparrow, home-range size (because this species is not strictly territorial) of northern males is much larger than that of birds in southern populations (Gilbert 1981). Within a region, habitat quality is important in determining the amount of clumping in territories. Post (1974) found the tendency to form high-density territory clusters was more pronounced in unaltered than in ditched marshes. Olsen (unpubl. data) compared territory size in Swamp Sparrows (*Melospiza georgiana*) in marshes with different levels of topographic relief created by muskrat (*Ondatra zibethicus*) activity. The more hummocky marsh supported clustered territories as small as 60 m², where the less topographically diverse swamp had a much more evenly distributed set of larger (≈ 1 ha) territories.

Clumping of territories is not restricted to passerines, because Clapper Rails are reported to have highly variable territory sizes with some as small as 0.1 ha, and the distribution has been described as colonial suggesting territory clustering (Eddleman and Conway 1998). The tendency to aggregate is well developed in the

non-territorial sharp-tailed sparrows (Greenlaw and Rising 1994). Nesting females (and hence competing males as well) tend to aggregate in what has been described as a colonial system.

Separation of nesting and feeding areas

At least eight of 11 saltmarsh species show a tendency to have separate feeding areas and nesting territories (Table 1). Of the non-saltmarsh relatives, only one of 11 species, the Red-winged Blackbird (Table 2), has been shown to have such a pattern of breeding season space use. In the case of Seaside (Post 1974) and Song sparrows (Grenier and Nordby, unpubl. data), as well as Clapper Rails, shared feeding areas are in more open, less vegetated parts of the marsh itself (Eddleman and Conway 1998). The eastern Willet (*Catoptrophus semipalmatus*), however, has nesting territories of about 0.5–1 ha within saltmarshes, but often travels to nearby intertidal mudflats and beaches to forage (Howe 1982).

Non-territorial aggregations

Refuge from tidal flooding can greatly restrict available habitat for short periods of time. Some tidal vertebrates may occur in local aggregations during high waters. Sibley (1955), for example, reported finding a flock of >100 emberizid sparrows, predominantly Song Sparrows, along a levee in a south San Francisco Bay tidal marsh experiencing a flood tide. The formations of such aggregations would require immigration of sparrows from a fairly large area. Johnston (1955) subsequently noted that Song Sparrows in an undiked tidal marsh move within their normal winter home range to areas above the flood-tide level. Johnston suggested that the flocking is a facultative response to human-altered marsh hydrology. West Coast populations of Song Sparrows are generally not highly social in the winter, but do form flocks, particularly when snowfall restricts available habitat in the winter (Greenberg, pers. obs.). Therefore, Song Sparrows may be sufficiently plastic in their social behavior to respond to unpredictable events, such as tidal flooding in a human restricted habitat.

Fisler (1965), based on his experience with captive animals, found that the salt marsh harvest mouse (*Reithrodontomys raviventris*) displayed a generally less aggressive and more socially tolerant disposition than did the western harvest mouse (*R. megalotus*), which may be a behavioral adaptation to the frequent, but short-lived crowding that is imposed on the species. Johnston (1957) reported that

small mammals in San Francisco Bay marshes, including harvest mice, are able to escape the direct effect of flooding by climbing on emergent vegetation, and that crowding above the flood line is rare. Padgett-Flohr and Isakson (2003) showed that the tendency to clump in salt marsh harvest mouse was a seasonal phenomenon, occurring during the breeding and immediate post-breeding period, but that the mice tend to occur in aggregations associated with mid-saline conditions thus avoiding both extremes in salinity. This more persistent patchy distribution may also explain the high social tolerance found in this harvest mouse species. Finally, Harris (1953) found that both marsh rice rats (*Oryzomys palustris*) and meadow voles (*Microtus pennsylvanicus*) found refuge at muskrat houses and feeding platforms during extreme high tides in brackish *Spartina* marshes on the Chesapeake Bay.

The tendency to aggregate in high-marsh zones or near the marsh ecotone was demonstrated in the Suisan shrews (*Sorex ornatus sinuosus*; Hays and Lidicker 2000). During the winter, they live in distinct social groups consisting of a single adult male, several adult females, and sub-adults. Even when the adult male died, these units persisted. With the onset of the breeding season groups were integrated by outsider adult males, and the result was an almost complete change-over in group membership (Hays and Lidicker 2000). The same study found shrew population densities highest where the marsh bordered the adjacent grassland, and that wintering sub-adult males mostly occupied areas of the marsh below high-tide level.

The importance of refuges from flooding

Availability, exploitability, and perhaps in extreme crowding, the defensibility of temporary refuges in times of high waters may be one of the most significant resources for most marsh animals and probably more so for mammals than birds. The role of marsh-upland ecotone in providing temporary or even seasonal refuge needs to be examined as land development in many areas moves closer to the actual marsh edge. The necessity of refugia also varies with major stochastic events in addition to flooding. Although generally rare, saltmarsh fires (Gabrey and Afton 2000) and prolonged freezing with resulting ice floes both drastically change the vegetation profile for one to two seasons following the event (Post 1974). Several mammal studies suggest refuges are more important in unmodified marshes than in muted (tidal extremes mitigated due to dikes) marshes (Padgett-Flohr and Isakson 2003, Kruckek 2004).

Data for mammals indicate that apart from serving merely as temporary locations for high-water escape, these ecotonal areas apparently can function both as population sources and sinks. For example, juvenile marsh rice rats tend to be excluded from saltmarsh and are forced into the upland old-field vegetation at the marsh border (Kruckek 2004). Other studies have found that age and sex ratios in areas of peripheral to saltmarshes vary seasonally (Hays and Lidicker 2000), in response to flooding (Hays and Lidicker 2000), weather (Kruckek 2004), and sometimes in response to density (Geissel et al. 1988). Finding from these individual studies invite further research on social interactions and habitat use in tidal marsh-upland systems.

Interspecific territoriality and avoidance

Interspecific territoriality or interspecific avoidance is often associated with structurally simple environments, such as grasslands and marshes (Murray 1969). High food abundance of tidal marshes may initially attract individuals from a variety of species to feed in or colonize tidal marshes, but low-structural diversity provides few ways for generalized insectivores to diverge in their fundamental foraging niche. Furthermore, because selection in the form of nesting mortality is so high and because the source of the mortality is nearly identical regardless of species or even class, we would expect a higher level of intra-specific nest-site competition in tidal marshes as compared to other habitats.

The interactions between *Ammodramus* species provide the best example of interspecific dominance and avoidance. Seaside Sparrows are dominant to sharp-tailed sparrows, which they regularly chase and supplant from nesting areas. The average distance between nests of the two species is greater than within species even where abundance is in approximate parity (Post 1974). Seaside Sparrows also supplant sharp-tailed sparrows in shared feeding areas. Although sharp-tailed sparrows are not territorial, the behavioral evidence suggests that aggression from Seaside Sparrows may cause sharp-tailed sparrows to avoid certain nesting areas.

The aggressively mediated spatial segregation between these species may be unique among tidal-marsh sparrows, where generally only one species is found in a particular marsh. However, where Swamp and Seaside sparrows co-occur, territories show almost no overlap. This avoidance appears to be mediated by distinct yet subtle differences in vegetation preference rather than by behavioral interactions (R. Greenberg, pers. obs.).

Spatial exclusion and avoidance has been documented among several small mammals of saltmarshes. Based on inferences from capture patterns during a population crash of California voles (*Microtus californicus*), Geissel et al. (1988) proposed that the salt marsh harvest mouse is a fugitive species that avoids spatial overlap with the dominant vole populations. The pattern fits an included niche model where the more salt-tolerant harvest mice can always take refuge in the lower more saline marshes, but expand into higher, grassier marshes in the absence of voles. If this pattern of physiological tolerance and competitive interaction is correct, it is similar to the relationship between lower marsh and upper marsh and upland plants, where the competitively superior forms are less able to colonize more saline-marsh zones. Although the gradient underlying competition in this case appears to be marsh salinity, a similar pattern of avoidance has been described between upland populations of western harvest mouse and California vole, where habitat disturbance is the driving habitat feature (Blaustein 1980). In the latter species pair, evidence from trap avoidance suggests that harvest mice avoid the odor produced by voles. The avoidance behavior between voles and salt marsh harvest mouse reported by Geissel et al (1988) needs further investigation both based on field distributions and behavioral interactions in the laboratory. Other researchers have not found such segregation between the species (Padgett-Flohr and Isakson 2003).

Avoidance also occurs between more distantly related taxa. Seaside Sparrows tend to avoid areas dominated by rushes (*Juncus*) in marshes along the southern Atlantic and Gulf Coasts and avoid spatial overlap with marsh rice rats. The relationship between the two species is complex, however, because rice rats are also major predators on sparrow nests (Post 1981). Guttenspergen and Nordby (*this volume*) discuss a similar possible interaction between Marsh Wrens and other passerines (notably Song Sparrows). The egg-puncture behavior of Marsh Wrens discourages other birds from nesting in their vicinity. This phenomenon has been well documented in freshwater marshes (Picman 1984).

DISCUSSION

SOCIAL ADAPTATIONS IN TIDAL-MARSH VERTEBRATES

To support a hypothesis of social adaptation to tidal marshes, the basic question is to what extent are their social behaviors ancestral, i.e., behaviors carried over from their immediate non-marsh dwelling ancestors (Searcy et al.

1999); and to what extent are the behaviors we now observe in tidal-marsh-dwelling species derived? If new social patterns are consistently detected in tidal-marsh birds, then we need to determine if there are underlying, genetically based differences specific behavioral traits of if the differences reflect facultative shifts within the behavioral repertoire of the non-tidal-marsh population. Although a thorough phylogenetic analysis of social system patterns probably cannot be accomplished at this point, we can make some specific comparisons between tidal-marsh taxa and their sister taxa.

It is unclear if any consistent difference trend can be found in the comparison of mating systems between tidal-marsh forms and their relatives. Coastal populations of both species of sharp-tailed sparrows apparently share their non-territorial and polygynous mating system with the inland subspecies of the Nelson's Sharp-tailed Sparrows (Murray 1969), although our understanding of the social system of the latter remains sketchy. Further evidence that the Sharp-tailed Sparrow mating system is not a specialized adaptation to tidal marsh is the observation that the Aquatic Warbler (*Acrocephalus paludicola*), which breeds in European freshwater sedge-fern bogs, is the song bird with the social system most similar to the Sharp-tailed Sparrow (Schulze-Hagen et al. 1999). Similarly, Boat-tailed Grackles are not restricted to salt marsh for breeding and non-salt marsh populations show a similar social system to those in saltmarshes (Post et al. 1996). The fact that these unusual mating systems are shared between salt- and freshwater-marsh populations does not exclude the possibility that this social system evolved in tidal marshes and characterizes the inland population as a result of a very recent colonization event, but it does show that the factors that maintain it are probably shared between interior and coastal marshes. Finally, in Savannah Sparrow (*Passerculus sandwichensis*), polygyny has been reported for some non-saltmarsh populations (Rising 1989, 2001, Wheelwright and Rising 1993), but not for the saltmarsh subspecies (J. B. Williams, pers. comm.).

Polygyny is frequent, but does not prevail in tidal-marsh birds. Two studies of polygynous Marsh Wrens and Red-winged Blackbirds suggest that, harem sizes are smaller than for interior populations of the same species. Furthermore, it is now unclear how common polygynous systems are in marsh birds in general. Surprisingly few attempts have been made to synthesize data relating breeding systems to marsh habitats incorporating the entire New World fauna. The most complete survey was

published by Greenlaw (1989), which includes both North and South American species. Based on this geographically broader view, Greenlaw suggests that polygyny is not disproportionately represented in marshland passerines. Although polygyny prevails in marshland passerines in North America, monogamy is dominant in South America, and polygyny there is rare. Greenlaw also points out that in Europe the correlation between polygyny in bird species in general, and marshes in particular, is not evident (Von Haartman 1969; but see a more comprehensive recent analysis of one taxonomic group by Leisler et al. 2002). Greenlaw (1989) argues that the expectation that polygyny should be common in marshland passerine birds is based on the assumption that a single mechanism, i.e., female choice in relation to polygyny thresholds, determines the mating systems in marsh habitats. Greenlaw (1989) points out that much of the pattern found in North American birds is found in species of a single family, Icteridae. He further argues that multiple routes exist in the evolution of avian polygyny. Outside of North America, one cannot presume that an observed correlation between polygyny and marshes has any significance concerning the importance of particular mechanisms (e.g., female choice in relation to polygyny threshold) that can account for a given mating system).

A polygyny-threshold model for the development of polygynous systems in marsh birds relies upon their being high productivity (so that males can be emancipated from provisioning and other forms of parental care) and highly variable habitat quality or a distinct advantage for nest protection conferring to females for nesting in close proximity to conspecifics (Searcy and Yasukawa 1989). High food abundance and patchy distribution of females characterize monogamous tidal-marsh-dwelling Song, Swamp and Seaside sparrows. In tidal-marsh sparrows and grackles, the increase in local density of territorial males may prevent individual males from being able to defend territories of sufficient quality and size to attract multiple mates. Therefore, it appears that attempts to be polygynous would be swamped.

As stated above, territorial clumping and semi-coloniality does appear to be a consistent feature of the spacing behavior of saltmarsh passerines. However, such behavior has often been noted in marsh birds in general, and it is unclear if tidal marshes display an unusually high tendency toward this behavior. For example, the LeConte's Sparrow (*Ammodramus leconteii*; Lowther 1996), the closest living relative of the Seaside Sparrow and sharp-tailed sparrows is noted for often having very small

territories that can be patchily distributed in prairie marshes. Murray (1969), however, found based on a direct comparison on his northern-prairie study site, that Nelson's Sharp-tailed Sparrow was much more prone to display a semi-colonial distribution than the LeConte's Sparrow. The locally high densities found in coastal plain Swamp Sparrows are, if anything, more pronounced in inland populations of this species (Greenberg, pers. obs.).

Separation of nesting and feeding territories is well developed among tidal-marsh birds and probably reflects the ephemeral availability of productive of some inter-tidal microhabitats. In terms of the expression of this pattern in non-tidal marsh relatives, the LeConte's Sparrow apparently does not have separate feeding areas (Murray 1969, Lowther 1996); however, this species remains poorly studied. Separate feeding areas have also not been reported in other inland species of *Ammodramus* (Vickery 1996, Green et al. 2002, Herkert et al. 2002). Non-tidal populations of Song Sparrows also do not show a tendency to have shared feeding areas (Nice 1937, Arcese et al. 2002). Shared feeding areas are not known for the interior marsh-nesting populations of the Willett (Lowther et al. 2001). King Rails are not known to have shared feeding areas during the breeding season (Meanley 1992), but space use of this species is also poorly known.

At this point, the partial separation of undefended feeding areas and defended nesting territories does seem to be a consistent characteristic of tidal-marsh populations or species when compared to related non-tidal-marsh forms. This pattern of space use probably reflects the highly variable quality of marsh vegetation and location for providing nesting areas safe from flooding and predation and the fact that the best areas for reproductive activities are decoupled from areas that have the highest abundance of accessible food. In addition, it might reflect the fact that microhabitat selection for feeding is much more flexible (not being constrained by nest location) and can respond to the rapidly changing face of the tidal marsh.

Non-territorial scramble polygyny clearly distinguishes the social system of the sharp-tailed sparrows as the most derived and unusual of the tidal-marsh-breeding species. As Greenlaw (1989) suggests, the underpinning of the system is that neither potential nesting areas for females or females are economically defensible. As a working hypothesis this system may be viewed as an endpoint in the tendency of tidal-marsh females to form nesting aggregations, to the point where the density of territorial males and non-territorial intruders prevent males

from defending territories. With no unique territorial resources, males must compete directly for access to receptive females. However, other saltmarsh sparrows occur in high densities with males being able to maintain nesting territories. The additional factor in the sharp-tailed sparrow system may be the species social subordination to congeners. This may force congregations in certain habitat types and the presence of clusters of non-territorial males may minimize the ability of other species to dominate individual sharp-tailed sparrows (Murray 1971, 1981). In this sense, the sharp-tailed sparrow system seems to be an endpoint for various behavioral features expressed to varying degrees in other tidal marsh species. Boat-tailed Grackles represent, perhaps, another extreme where colonial females are economically defensible because dominant males can easily repel competitors and predators from the colony site.

DIRECTIONS AND OPPORTUNITIES FOR FURTHER RESEARCH ON THE EVOLUTION OF SOCIAL SYSTEMS OF TIDAL-MARSH ANIMALS

As this paper shows, with the exception of a few well-studied species and populations, we are still in the descriptive stage in understanding social systems and behaviors of tidal-marsh vertebrates. At this time, the most detailed comparative information comes from birds, with less known about mammals and virtually nothing known about reptiles. Outside of more basic descriptive research, focusing on comparisons between tidal-marsh and related taxa, more conceptual areas of research exist for which tidal-marsh vertebrates should prove an interesting and tractable system.

The most salient feature of tidal-marsh social systems is the tendency to form aggregations of individuals or territories. The underlying fitness trade-offs associated with these patterns has only been occasionally explored. In particular, what is the nature of the trade-off between risk of flooding and lack of nesting cover on one hand, and the competition and density dependent increase in predation that might ensue from settling in crowded but safer habitats? How do uncoupled gradients in food availability, cover, and presence of high and unflooded substrates shape decisions on where to settle? Since a gradient of dispersion patterns is present in many of the taxa and the underlying habitat structure and floristics is relatively simple, the tidal-marsh system would provide excellent opportunities to examine the forces driving these patterns. This could be done both within and between populations and species to develop general hypotheses.

The consequences of these clumped spatial patterns in terms of other aspects of social behavior, particularly communication and mating systems, would be a fascinating area of inquiry. For example, how does the tendency to occur in very high local densities affect patterns of both short-distance and long distance acoustic signals in birds? It has been hypothesized that females give a nest-departure call in marsh or grassland environments where populations achieve high densities (McDonald and Greenberg 1991). We proposed that females need to communicate to their mates when they leave the nest to minimize aggressive harassment. Another question relating clumping behavior to communication is how the tendency to form dense aggregations shapes the relationship between males and females and the dynamics of extra-pair mating. Surprisingly, we know almost nothing about the actual genetic contribution of different males and females to their putative offspring for any of the terrestrial tidal-marsh vertebrates.

In addition to the social environment, tidal marshes offer an opportunity to study how the physical environment might shape communication signals (Morton 1975, Wiley 1991). The presence of locally differentiated populations allows comparative work on how the structure of the environment and the local microclimate might shape acoustic signals in birds. This could be accomplished through detailed analysis of the signal and reciprocal playback experiments using recorded vocalizations from tidal-marsh and inland populations. Furthermore, the mode of signal presentation, e.g., frequency of vocalization, use of perches, and use of flight songs should be a fruitful area of inquiry.

Reliance on scent communication should be modified in tidal-marsh dwellers due to the daily inundation of water that could dilute or dissolve olfactory cues. Three sets of predictions, not necessarily mutually exclusive, can be generated and are open for investigation due to no known data on the subject: (1) scent trails and markers are chemically adapted so as to be less prone to water wash-out, and also

perhaps resistant to chemical alternation by saline solutes, (2) scent use is relied on less, in general, in tidal-marsh animals as compared to their non-marsh counterparts, and (3) scent application and function use in navigation and communication are temporarily adapted to tidal cycles, e.g., preferentially placed on stems above high-tide levels, or relied on as reproductive readiness cues during the middle of the lunar cycles.

Given the simple habitat structure and often high abundance achieved by a few dominant species, tidal marshes clearly provide a good system for investigating interspecific behavioral partitioning of space. In particular, the avoidance behavior hypothesized between some species of small mammals would be an opportune focus for integrated ecological work on patterns of distributions and behavioral studies of interspecific dominance and communication.

Finally, most research on social behavior has focused on breeding-season events. Only the broadest picture is available for the social interactions of vertebrates during the non-breeding season. The pattern of resource availability may be most distinct between tidal-marsh and upland habitats at this time of year. Future integrations of our understanding of non-breeding and breeding social systems in migratory and non-migratory populations will contribute to this rapidly growing area of ornithological research.

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