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OSMOREGULATORY BIOLOGY OF SALTMARSH PASSERINES

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Abstract. In North America, several taxa (species or subspecies) of sparrows in the family Emberizidae are characteristic of saltmarshes. The fact that recognizable avian taxa are associated with, and perhaps restricted to, saltmarshes suggests that these habitats impose significant selective pressures. A likely candidate for this selective agent is the demand placed on homeostasis by a limited supply of fresh water and a possibly high intake of salt. A number of studies in the laboratory document that saltmarsh sparrows differ from their upland conspecific relatives. Saltmarsh residents tend to drink more, to tolerate saltier water, and to diminish drinking rates at high salt concentrations, in contrast to non-saltmarsh birds. The kidneys of sparrows from saltmarshes are large, enhanced particularly in medullary mass associated with an increased number of nephrons with loops of Henle. They may also have enhanced urine concentrating ability. These features are consistent with expectations for birds that drink salty water. Nevertheless, little evidence exists that such intake actually occurs in the field; just a single study has indicated an increased urine flow in birds freshly captured in the field, and direct measures of water or sodium intake that could corroborate this hypothesis are lacking. Studies of physiological function in the field, and of the relative roles of inheritance versus environment in determining osmoregulatory capabilities in birds, would help to resolve the question of how important osmoregulation is in restricting saltmarsh sparrows to that habitat.

Key Words: Avian kidneys, Emberizidae, *Passerculus*, salinity tolerance, saltmarsh birds.

BIOLOGÍA OSMOREGULATORIA DE COLORINES DE MARISMA SALADO

Resumen. En Norte América, varias taxa (especies o subespecies) de gorrión en la familia Emberizidae son características de marismas saladas. El hecho de que taxa avícola reconocible se encuentre asociada con, y quizás restringida a marismas saladas, sugiere que estos habitats imponen presiones selectivas significativas. Un candidato parecido para este agente selectivo es la demanda localizada en homeostasis por un limitado suministro de agua fresca y una posible toma alta de sal. Un número de estudios en el laboratorio documentan que los gorriones de marisma salada difieren de sus parientes conespecíficos de tierras más altas. Los residentes de marismas saladas tienden a beber más, para tolerar aguas más saladas, y tienden a disminuir las proporciones de beber a unas concentraciones altas de sal, en contraste a las aves que no son de marismas saladas. Los riñones de los gorriones de marismas saladas son más largos, amplificados particularmente en la masa medular, asociada con un número incrementado de nefrones con lazos de Henle. Quizás también hayan aumentado su habilidad de concentración de urina. Estas características son consistentes con las expectativas de aves que beben agua salada. No obstante, existe poca evidencia de que dicha entrada de hecho suceda en el campo; solo un estudio ha indicado un flujo incrementado de urina en aves recientemente capturadas en el campo, y mediciones directas de entradas de agua y sodio, lo cual comprueba de lo que carece esta hipótesis. Estudios de función fisiológica de campo, y lo relacionado a los roles relativos de herencia contra ambiente para determinar las capacidades osmoregulatorias de las aves, ayudaría a resolver la pregunta de qué tan importante es la osmoregulación en restringir gorriones de marismas salados al habitat.

Because most tidal marshes are inundated with sea water, one of the fundamental adaptive challenges for successful colonizing organisms is the ability to tolerate salty fluids or to find alternative sources of water. Among vertebrates, the ability to survive these conditions may derive from three classes of traits, which roughly reflect the degree of specialization to marine life (Dunson and Travis 1994). First, many organisms rely on behaviors that minimize their exposure to or intake of salt water. For example, species and subspecies of water snakes avoid drinking salt water, relying instead on fluids obtained from osmoregulating prey items (Pettus 1958, Dunson 1980). Likewise, the herbivorous meadow vole (*Microtus pennsylvanicus*), which apparently can not tolerate ingesting salty water, satisfies its water needs by consuming dew and precipitation and selectively eating grasses with low salt content (Getz 1966). Second, physiological adaptations may be based on existing organs and structures. Examples of this strategy include integumentary adaptations in some estuarine snakes and turtles that reduce the fluxes of sodium and water between animal and environment (Dunson 1980). Likewise, adaptations in kidney structure and function may allow certain saltmarsh forms of mice (Fisler 1962, 1963; MacMillen 1964) and sparrows to better tolerate ingesting saline water. Finally, the most specialized marine forms have evolved novel features—in particular, salt glands—that help to produce and excrete a concentrated salt solution. Salt glands are normally associated with completely marine forms, but are also found in some estuarine and saltmarsh residents like rails (Olson 1997), crocodiles (Dunson and Mazzotti 1989), and diamondback terrapins (*Malaclemys terrapin*; Robinson and Dunson 1976, Hart and Lee, *this volume*).

Although saltmarshes tend to be relatively low in biodiversity, some groups of organisms show particularly high levels of evolutionary success in occupying these ecosystems. Passerines, particularly New World sparrows in the family Emberizidae, are one such group that has repeatedly invaded coastal marshes throughout the Pleistocene (Chan et al., *this volume*). To help understand how they have achieved this success requires exploration of the details of salinity tolerance or avoidance. In this paper I examine the possible adaptations that might underlie the success of saltmarsh sparrows.

THE CHALLENGE POSED TO BIRDS BY SALTMARSHES

Birds and mammals are the only vertebrates capable of producing urine that is hyperosmotic to plasma. In both groups this capability derives from the presence of loops of Henle in the kidneys. These structures are part of a counter-current multiplication system that generates a renal medullary osmotic gradient, and this gradient is used to extract water from the urine.

Despite sharing this physiological and anatomical basis of function, birds and mammals differ in their ability to concentrate urine. In mammals, maximum urine concentration is typically >1,000 mosM and may reach seven times this value in small desert rodents, more than 25 times the concentration of blood plasma (Beuchat 1990). In contrast, birds typically can concentrate urine only to 600–1,000 mosM, two–three times plasma osmolality (Goldstein and Braun 1989). Moreover, this maximum avian urine concentration is no more concentrated than seawater, with a concentration of about 1,000 mosM (Fig. 1).

For birds living in saltmarshes, the available water is saline, sometimes even more concentrated than seawater (Fig. 1). The question arises: can birds tolerate drinking these saline waters? Birds obligatorily lose body water through respiratory and cutaneous evaporation. Thus, it would seem that if a bird drank seawater, sole reliance on urinary excretion of ingested salts would impose a net water loss. This is the dilemma facing passerine birds inhabiting saltmarshes.

Despite this, a number of passerine taxa are characteristic inhabitants of North American saltmarshes. The Seaside Sparrow (*Ammodramus maritimus*) and Saltmarsh Sharp-tailed Sparrow (*A. caudacutus*) are the species most associated with saltmarshes. In several other species, recognizable subspecies of otherwise freshwater or upland species are saltmarsh inhabitants. These include representatives of the Savannah Sparrow (*Passerculus sandwichensis*), Nelson's Sharp-tailed Sparrow (*Ammodramus nelsoni*), Song Sparrow (*Melospiza melodia*), and Swamp Sparrow (*Melospiza georgiana*), all members of the Emberizidae. In South America, species of *Cinclodes* in the family Furnariidae are found along shorelines, where they include osmoconforming marine mollusks in their diet and likely incur substantial seawater loads. The physiological features of these species, many of which may be shared with emberizids, are just beginning to receive study (Sabat 2000, Sabat and Martínez Del Rio 2002). Here, I restrict discussion to the emberizids of North American saltmarshes.

The fact that recognizable avian taxa are found associated with, and perhaps restricted to saltmarshes, suggests that these habitats impose significant selective pressures. This supposition is further supported by the observation that some behavioral, morphological, and physiological traits are shared by a number of saltmarsh taxa (Bartholomew and Cade 1963, Greenberg and Droege 1990). Thus, some suite of factors apparently induces taxonomic differentiation, largely restricts saltmarsh sparrows to saltmarshes, and constrains other forms of these same species from colonizing saltmarshes. One candidate for this selective agent is the demand placed on homeostasis by a limited supply of fresh water and a possibly high intake of salt. For example, Greenberg and Droege (1990) note that even tidal-marsh Swamp Sparrows (*Melospiza georgiana*) do not breed in areas with waters >50% seawater concentration.

SALT GLANDS: A POTENTIAL (BUT MISSING) SOLUTION

Cephalic salt-excreting glands that compensate for the limited urinary concentrating ability have evolved in many birds that live in marine environments. These glands are capable of secreting solutions of nearly pure NaCl at concentrations that may exceed those of seawater. Included among the avian orders with salt glands are the truly marine groups, like Procellariiformes and Sphenisciformes, and those that are more sporadically or facultatively marine, such as Charadriiformes, ducks, and herons. Functional salt glands also occur in

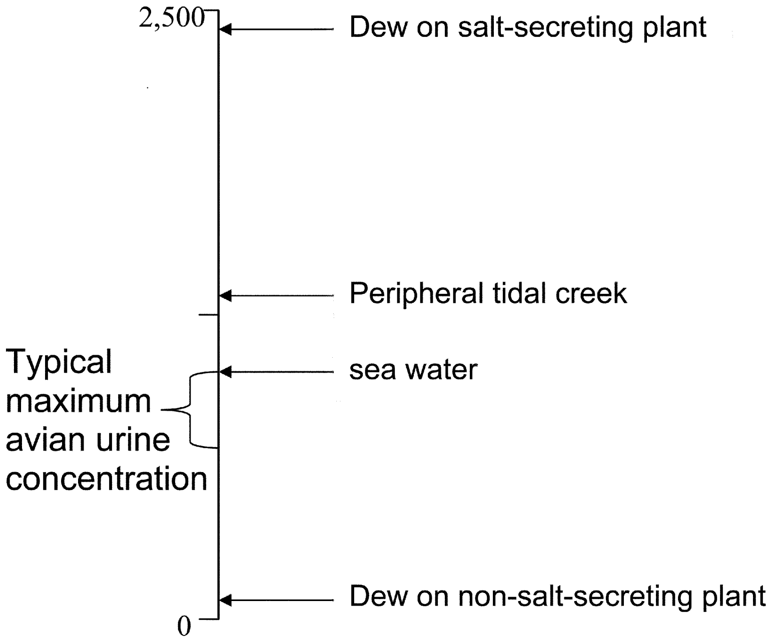

FIGURE 1. A comparison of the concentrations of water sources in a tidal marsh (measured at Bahia San Quintin, Baja California, Mexico; Goldstein et al. 1990) with the concentrating ability of the avian kidney.

some non-aquatic species, like young roadrunners (*Geococcyx*; Ohmart 1972) and several Falconiformes (Cade and Greenwald 1966). However, passerines lack functional salt glands; even those inhabiting saltmarshes or marine shores must rely on the kidneys and intestinal tract for eliminating dietary salt.

OTHER MORPHOLOGICAL FEATURES

At present, morphological attributes are used to distinguish subspecies of saltmarsh sparrows. These features are shared by several taxa (Greenberg and Droege 1990). Saltmarsh sparrows tend to have large, narrow beaks and have less rusty coloration in their plumage. It is not clear—indeed, it is unlikely—that any of these features have a role in osmoregulation. In some birds that feed on marine foods, beak morphology is specialized to function as a filter, limiting the intake of salt water (Mahoney and Jehl 1985, Janes 1997). No evidence, however, supports this function for the large beaks of saltmarsh sparrows.

DRINKING

Water Consumption in the Laboratory

The consumption of salty water has been evaluated in several species of saltmarsh sparrows. Patterns appear to be similar whether drinking diluted seawater or solutions of NaCl (Basham and Mewaldt 1987). Bartholomew and Cade (1963) delineated general patterns of drinking rate in response to increasing salinity of the water. Like their upland relatives, saltmarsh sparrows given a choice of fresh or saline water typically prefer fresh water and consume relatively small quantities of saline (Bartholomew and Cade 1963, Poulson 1969). However, when given just a single drinking solution, whether fresh water or saline, saltmarsh residents tend to drink more water than non-saltmarsh sparrows (Bartholomew and Cade 1963; Figs. 2 and 3). Moreover, the saltmarsh birds generally decrease consumption as salinity increases. (See Fig. 3 for an exception to these generalizations). Saltmarsh sparrows can maintain body mass when drinking more highly concentrated salt solutions than is tolerated by non-saltmarsh forms.

Saltmarsh and non-saltmarsh sparrows differ in the relation between drinking rate and tolerable saline concentration (Fig. 4). Non-saltmarsh sparrows drink maximally at saline concentrations above the maximum they can tolerate; that is, they increase consumption even while incurring a net loss of body water (and hence body mass) apparently in an effort to excrete the ingested salt. In contrast, saltmarsh sparrows drink maximally at concentrations

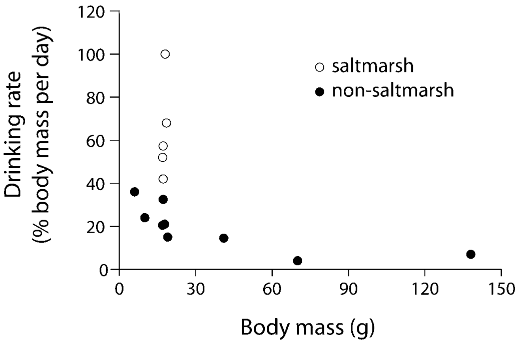

FIGURE 2. Freshwater drinking rates in saltmarsh emberizids (open circles) compared with other birds (filled circles). The five highest drinking rates are saltmarsh emberizids. Data from Bartholomew and Cade (1963).

below the highest they can tolerate, and at least some can maintain body mass even while drinking NaCl solutions with osmolality equivalent to full-strength seawater.

It is also possible that saltmarsh sparrows actually require more salt in their diet. Large-billed Savannah Sparrows (*Passerculus sandwichensis rostratus*) were able to resist desiccation, as evidenced by maintenance of body mass, much better after drinking seawater for several days than after drinking distilled water (Cade and Bartholomew 1959). This effect could derive from an elevated obligatory salt loss, perhaps resulting from an enhanced abundance of salt-wasting unlooped nephrons in the kidneys, and this might contribute to the restriction of saltmarsh taxa to that habitat. It is not known whether the differences in drinking patterns between saltmarsh and non-saltmarsh sparrows are genetically encoded or perhaps induced by environmental factors such as salt intake during growth.

WATER CONSUMPTION UNDER NATURAL CONDITIONS

In the laboratory, saltmarsh sparrows drink relatively large volumes of salt water. Does this occur also in the field? Poulson (1969) argued that the correlation between urine concentrating ability and salinity of waters available in the field does suggest that free-living saltmarsh passerines are likely to acquire much of their water intake from saline waters. Yet evidence to support this view is lacking. Indeed, Williams and Dwinnel (1990) reported that they had not observed Belding's Savannah Sparrows (*Passerculus sandwichensis beldingi*) drink seawater in the field.

Measures of energy and water flux have been used to estimate drinking rates in the field in one subspecies of saltmarsh passerine,

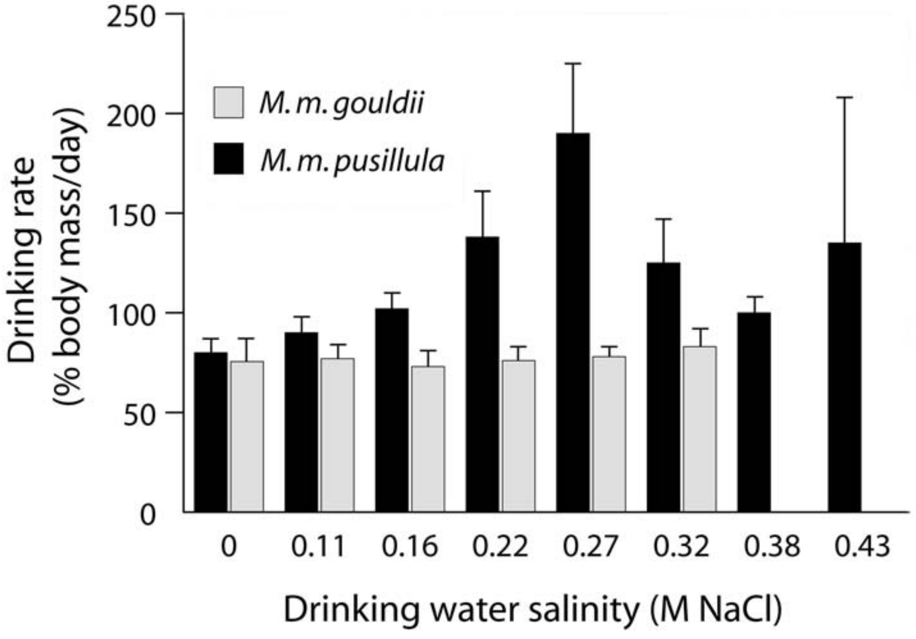

FIGURE 3. Drinking rates of two subspecies of Song Sparrow (*Melospiza melodia pusillula* [saltmarsh resident; solid bars] and *M. m. gouldii* [non-saltmarsh resident; open bars]) given solutions of varying NaCl concentration in the laboratory. Data from Basham and Mewaldt (1987).

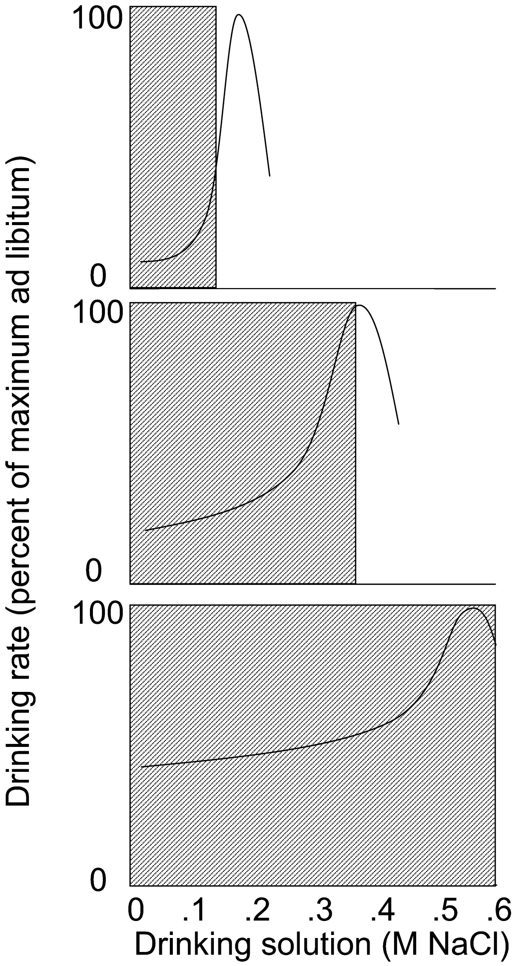

FIGURE 4. Generalized patterns of drinking in response to varying molarity of NaCl in the drinking water. Patterns are depicted for birds ranging from less salt-tolerant (top panel) to more salt-tolerant (lower panel). The solid line represents the pattern of drinking; the hatched regions indicate the range of salinities over which the birds can maintain body mass (Poulson 1969).

Belding's Savannah Sparrows inhabiting the saltmarshes of Baja California (Williams and Dwinnel 1990). In these birds, total water fluxes in the field, including water intake deriving from drinking, feeding, and oxidative metabolism, have been measured from the turnover of tritiated water. These water turnover rates are similar to those predicted from the allometry of water turnover rates in a variety of non-saltmarsh species (Williams et al. 1993). Energy intake in these birds was also measured using doubly labeled water (Williams and Nagy 1984, 1985; Speakman 1997). This measure, combined with an analysis of the water and energy content of their diet, was used to estimate water intake from sources other than drinking. The result suggested that diet and metabolic water could account for all but about 3.5 ml of water intake. The authors conjectured that this additional water may have derived from sparrows drinking dew (Fig. 1), which was available each morning.

Other methods that might yield further insight into drinking patterns in the field include the simultaneous measure of water and sodium fluxes (Goldstein and Bradshaw 1998), analysis of osmotic concentrations of gut contents (Sabat and Martínez del Rio 2002), and diet analysis using stable isotopes (Sabat and Martínez del Rio 2002). Studies at times of year other than the breeding season might also prove instructive. None of these approaches has been applied to saltmarsh sparrows. Still, field-caught birds have osmoregulatory organs that appear to be suited for a high intake of salt and water. Together with the data on drinking in the laboratory, it remains a reasonable conjecture, though undocumented, that saltmarsh sparrows in the field consume salty water.

FOOD SELECTION

Foods available to sparrows in saltmarshes are likely to vary substantially in salt content. Foods taken directly from the vegetation, including seeds and insects, are probably no more salty than those found in other, non-marine, habitats. On the other hand, some saltmarsh plants do actively excrete salt onto their surfaces, and invertebrates like crustaceans, mollusks, or annelids that live in the briny waters are likely to osmoconform with those waters and so have elevated salt content (Withers 1992). Thus, choice of diet may well dictate the salt load ingested.

Data on diet choice in saltmarsh sparrows suggest significant variability both within and among species. For example, during the breeding season the Saltmarsh Sharp-tailed Sparrow consumes mostly animal foods, including large proportions of insects but also amphipods (23.7%) and mollusks (3.6%) that could have more marine-like body fluids. In contrast, this same species switches to 30% plant parts during non-breeding months (Greenlaw and Rising 1994). Invertebrates can vary substantially in salt content. For example, terrestrial mollusks (e.g., terrestrial snails) may be water rich and low in salt, whereas marine gastropods have body fluids as concentrated as seawater; proper identification of such prey is critical to evaluating the osmoregulatory implications of diet choice.

MIGRATION AND SEDENTARINESS

The migratory habits of saltmarsh sparrows vary. Some, like Saltmarsh Sharp-tailed Sparrows and northern populations of Seaside Sparrows, are migratory. Notably, though, even when they leave their northern breeding grounds for regions further south they remain in tidal marsh habitat. Tidal-marsh populations of Swamp Sparrows also leave their breeding grounds in the autumn, but remain in tidal marshes along the Carolina coast (Greenberg et al., in press). For several other species, though, the saltmarsh sparrows are sedentary. This is true for the coastal populations and subspecies of Song Sparrows and Savannah Sparrows, and it is also true for southern populations of Seaside Sparrows. Indeed, for Savannah Sparrows, the saltmarsh variants are among the only non-migratory subspecies, although some Large-billed Savannah Sparrows are known to move north and out of saltmarshes in the winter. The sedentary habits of many saltmarsh sparrows may have evolved in association with the contraction of saltmarsh habitats, along with the physiological specialization of the birds. The strict association with saltmarshes also implies an inability to invade other habitats. The extent to which this results from osmoregulatory constraints is not resolved.

EXCRETORY ORGANS

Kidneys

Kidney structure

Birds have unique kidneys, with structures intermediate between reptilian and mammalian. As noted above, their ability to produce urine that is hyperosmotic to plasma derives from the presence of a renal medulla containing loops of Henle. However, only some avian nephrons, 25% or fewer, possess these loops, and the great majority are unlooped and therefore unable to concentrate urine (Goldstein and Braun 1986, 1989). The proportions and numbers of these nephron types vary among species (Goldstein and Braun 1989). What might one hypothesize for saltmarsh birds?

Kidneys of saltmarsh birds should have high populations of loopless nephrons. As noted above, these relatively short and simple nephrons do not contribute to the urine concentrating ability and might be thought of as water and salt wasting. Thus, to cite an extreme example, some hummingbirds, which ingest highly dilute nectar and must excrete water loads while conserving scarce electrolytes, have few or no loops of Henle (Beuchat et al. 1999). In contrast, arid-adapted species, which must conserve water, appear to have a reduced proportion of loopless nephrons (Thomas and Robin 1977). One might expect that in this regard saltmarsh species would more closely resemble hummingbirds—they need to excrete substantial volume loads, judging from their high drinking rates in the laboratory, and thus their kidneys should feature a large number of loopless nephrons (though see Sabat and Martínez del Rio [2002] for a possible contrary example).

Saltmarsh birds also should have substantial numbers of nephrons with well developed loops of Henle. In contrast to hummingbirds, the fluids ingested by saltmarsh sparrows may contain abundant electrolytes. Ingestion of hyperosmotic fluids would require the concentrating ability conferred by looped nephrons. Thus, if saltmarsh birds rely on salty drinking water they would require the features of both loopless and looped nephrons, and an abundant representation of both nephrons types should result. Together, this implies that saltmarsh passerines should have relatively large kidneys.

The morphology of individual nephrons also is variable. In particular, the principle of a countercurrent multiplier predicts that longer loops of Henle should confer a greater ability to generate a medullary osmotic gradient, and thereby a greater ability to extract water and concentrate the urine. Birds that ingest saline waters and lack salt glands therefore might be expected to have long loops of Henle, permitting solutes to be excreted in a minimal water volume. Overall, then, we predict large kidneys with long loops of Henle in these species.

Aspects of kidney structure have been evaluated in several populations of saltmarsh Savannah Sparrow (Table 1; Poulson 1965, Johnson and Ohmart 1973, Johnson 1974), and preliminary reports for *Cinclodes* suggest parallel findings. Kidney mass is relatively large in saltmarsh passerines, at least in part from an enlargement of the renal medulla (Casotti and Braun 2000). This translates into high values of relative medullary thickness (medullary length relative to kidney mass), an index used to compare medullary development across species (Johnson 1974). Interestingly, this enlargement appears to entail an increase in the number of medullary cones, but not in their length (Poulson 1965). It is less clear whether the large kidney size also reflect a large mass of cortical tubule elements. In a comparison across species, Belding’s Savannah Sparrows had similar cortical mass (including elevated mass of proximal tubules and reduced distal tubules) compared with House Sparrows

TABLE 1. ASPECTS OF KIDNEY MORPHOLOGY IN SALTMARSH AND NON-SALTMARSH SPARROWS.

	Upland sparrow [a]	Saltmarsh Savannah Sparrow (*Passerculus sandwichensis beldingi*)[a]
Kidney mass (g)	0.21	0.34
Relative number of medullary cones [b]	10	20
Medulla volume (mm^3) [c]	6.8	15.2
Relative length of Henle's loop [d]	2.6	2.5

Note: Data from Poulson (1965), Johnson and Mugaas (1972), Goldstein et al. (1990), and Casotti and Braun (2000).

[a] Upland sparrows include Song Sparrows (for medullary volume) and, for the other three variables, Savannah Sparrows (*Passerculus sandwichensis brooksi* and an unidentified subspecies). The Savannah Sparrow varieties did not differ in body mass.

[b] Medullary cone abundance expressed as the number of units of medullary cone seen per histological section of kidney, as described by Poulson (1965).

[c] Song Sparrows and Savannah Sparrows had nearly identical total kidney volumes, 129.4 and 129.8 mm^3, respectively (Casotti and Braun, 2000).

[d] Relative length calculated as (mean length of the medullary cones × 10) divided by the cube root of kidney volume. See Johnson (1974).

(*Passer domesticus*) and Song Sparrows (Casotti and Braun 2000). Intraspecific analyses of these variables, e.g., comparing saltmarsh and non-saltmarsh Savannah Sparrows, are not available. Thus, saltmarsh passerines have kidney structures only partly consistent with predictions. Nevertheless, the large kidneys, incorporating well-developed cortex and medulla, are most consistent with expectations for handling large amounts of ingested salt water.

Kidney function in the laboratory

Only a few measures of excretory function have been made in saltmarsh sparrows. These entail the collection of fluid voided by birds drinking water of different salinities. Because the ureters empty into the posterior intestine in birds, where urine composition can be modified even at high urine flow rates (Laverty and Wideman 1989), voided fluid probably does not represent the output of the kidneys.

The most notable finding in these studies is a report that Belding's Savannah Sparrows drinking 0.6 M NaCl excreted a fluid with a Cl^- concentration of 960 meq/L and a total osmolality of ~2000 mosmol/kg, more than five times the mean plasma osmotic concentration (Table 2; Poulson and Bartholomew 1962). This is the highest osmolality reported for avian urine and is often quoted in the literature. Nevertheless, I am cautious about this datum—birds in this experiment had variable plasma osmolalities, including values up to 610 mosmol kg^{-1}, far above normal. They were also drinking copious volumes of saline (about 20 ml d^{-1}) and it is possible that fluid could have passed through the gut without full absorption, so that excreted fluid represented a mix of urine and this gut fluid. No other aspects of renal function have been evaluated in saltmarsh sparrows.

Kidney function in the field

A single study has explored renal output from saltmarsh sparrows in the field (Table 3; Goldstein et al. 1990). Belding's Savannah Sparrows in the tidal marshes of Baja California produced relatively copious urine flow, about five times that produced by an upland subspecies of Savannah Sparrow captured at the same time in the scrub surrounding the marsh. The osmotic concentration of this urine was also about 20% higher in the saltmarsh birds, but in no case near the maximal values reported by Poulson and Bartholomew (1962).

LOWER INTESTINE

In birds, urine empties from the ureters into the cloaca, from where it may move by reverse peristalsis into the colon (Goldstein and Skadhauge 1999). The colon has the ability to modify the urine in a variety of ways, including uptake of organic molecules, transport of electrolytes between blood and lumen, and reabsorption or secretion of water. Moreover, the capacities, characteristics, and structural

TABLE 2. URINE CONCENTRATING ABILITY IN SELECTED PASSERINES.[a]

Species	Maximum urine/plasma osmotic ratio
Saltmarsh Savannah Sparrow (*Passerculus sandwichensis beldingi*)	5.8 (see text)
Non-saltmarsh Savannah Sparrow (*Passerculus sandwichensis brooksi*)	3.2
House Finch (*Carpodacus mexicanus*)	2.4
Zebra Finch (*Taeniopygia guttata*)	2.8

[a] Data from Poulson and Bartholomew (1962) and Goldstein and Braun (1989).

TABLE 3. URINE PRODUCTION BY SALTMARSH AND UPLAND SAVANNAH SPARROWS.[a]

	Saltmarsh	Upland
Urine flow (μl/h)	500	100
Urine osmolality	575	485
Plasma osmolality	350	340

[a] Data from Goldstein et al. (1990).

bases of these transport functions are altered in response to dietary salt content. In the chicken (*Gallus gallus*), for example, birds on low-salt diets have enhanced capacity for lower intestinal salt absorption, the absorption becomes insensitive to the presence of organic substrates like amino acids and glucose, and the gut surface area is magnified by the development of an extensive apical brush border (Table 4; Elbrønd et al. 1993).

The responsiveness of the lower intestine of saltmarsh sparrows to salt intake under controlled conditions remains little studied. However, Savannah Sparrows of Baja California provide an illustration of these patterns under field conditions (Goldstein et al. 1990). Belding's Savannah Sparrow, the saltmarsh resident, had a colonic epithelium with relatively smooth mucosal surface, providing a small surface area indicative of a low transport capacity as would be expected if electrolytes were abundantly available. In contrast, birds of a presumably migratory, non-saltmarsh subspecies found at the same time in nearby upland habitat had colonic epithelia with extensive micro-villous folding on the mucosal surface, providing substantial re-absorptive surface area as needed for salt conservation (Fig. 5). Again, these findings provide indirect evidence that saltmarsh sparrows have elevated salt intake.

OSMOREGULATION IN SALTMARSH MAMMALS

As noted in the introduction, passerine birds are not the only terrestrial vertebrates that might be challenged by the osmoregulatory demands of saltmarshes. Because mammals are the only non-avian vertebrates capable of producing urine that is hyperosmotic to plasma, it may be instructive to examine the role of salt tolerance in the distributions of mammalian saltmarsh races and species. Several taxa of small rodents—species or subspecies—inhabit and appear to be restricted to these environments (Shellhammer et al. 1982, Woods et al. 1982, Bias and Morrison 1999). One might hypothesize that a salty environment would be less of a challenge to homeostasis in small mammals than in birds. Small rodents typically can concentrate their urine to several times the osmotic concentration of seawater (Beuchat 1990), and a substantial component of mammalian urinary solutes is NaCl. Thus, even if the rodents drank saline water they should be able to eliminate the salts in a lesser volume, resulting in a net gain of pure water. Indeed, work by MacMillen (1964) on western harvest mice (*Reithrodontomys megalotis*) and Fisler (1963) on salt marsh harvest mice (*R. raviventris*) showed that rodents from saltmarshes can survive drinking sea water. Upland subspecies of *Reithrodontomys* may (Fisler 1963) or may not (MacMillen 1964) be less tolerant of highly saline solutions than their saltmarsh counterparts. Nevertheless, several studies suggest that salinity does limit the distribution of small mammals in saltmarsh environments. For example, meadow voles cannot tolerate water with salt concentrations >50% sea water, and Getz (1966) suggested that selective herbivory of plants with lower salt concentrations, as well as the use of dew, allows voles to occupy saltmarshes.

Physiological features other than tolerance of simple NaCl solutions may well contribute to these patterns. California voles (*Microtus californicus*) in saltmarshes were better able to ingest succulent halophytes like *Salicornia* than seemingly more salt tolerant cricitid rodents, perhaps because of special features of the digestive processes (Coulombe 1970). Moreover, in contrast to the results of laboratory drinking experiments, harvest mice were averse to eating plants with high salt content, perhaps because they contained cathartic ions (Coulombe 1970). Thus, food selection and use of dew as a water source may be important mechanisms for tolerating the saltmarsh environment; torpor may allow mammals to survive periods of osmoregulatory stress.

TABLE 4. THE EFFECT OF HIGH- VS. LOW-SALT DIET ON LUMINAL MORPHOLOGY OF THE HEN LOWER INTESTINE (COPRODEUM).[a]

	High NaCl diet	Low NaCl diet
Na transport	0–1 μmol/cm2h	7–12 μmol/cm2h
Apical surface area	86 cm^2	202 cm^2
Number of microvilli	35 × 109	71 × 109
Length of microvilli	7,289 m	19,738 m

[a] Data from Elbrønd et al. (1993).

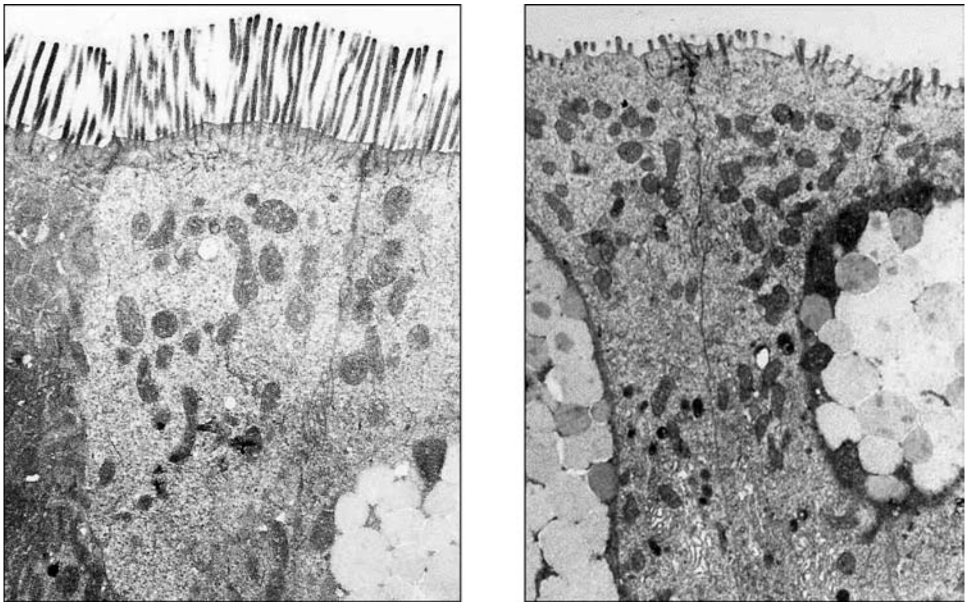

FIGURE 5. Electron micrographs of colons from upland (left) and saltmarsh Savannah Sparrows. Note in particular the enhanced elaboration of the microvilli in upland birds, associated with their greater need for intestinal salt uptake.

CONCLUSIONS

Species, subspecies, and populations of several emberizid sparrows are resident in North American saltmarshes. The fact that these taxa are distinct from conspecifics residing outside of saltmarshes suggests that one or more selective agents have induced differentiation in these habitats. Moreover, the sedentary habits of many of these taxa suggest that they may be constrained from leaving the saltmarshes, and perhaps that non-saltmarsh taxa are unable to invade. In this review, I have examined the evidence that osmoregulatory demands, associated with a dearth of fresh water, an abundance of salt, or both, may be the selective agent acting on these birds.

Overall, evidence from laboratory studies indicates that the osmoregulatory biology of saltmarsh sparrows is specialized. Saltmarsh residents drink and tolerate more salty drinking solutions. Moreover, several lines of evidence from the field, including urine flow rates and morphological features of osmoregulatory organs, provide circumstantial evidence for intake of salt water in the field. Direct evidence for that intake is lacking.

The question remains as to whether the osmoregulatory capacities of saltmarsh birds restrict them to those habitats. At least one study implies that saltmarsh sparrows may actually require more salt in their diet, at least if they are to tolerate times of water restriction. A few studies of saltmarsh mammals indicate that other physiological challenges, such as effects of ions other than Na^+ and Cl^-, may be important. It remains unclear whether osmoregulatory physiology can explain the exclusion of non-saltmarsh taxa from the marshes. Other explanations, from food availability to social interactions, are also possible.

We also do not know the extent to which osmoregulatory features of saltmarsh sparrows are genetically determined. No one has yet attempted common garden experiments with and without salty diets, in which saltmarsh and non-saltmarsh birds are reared under common conditions.

Emberizid sparrows may be among the best indicator species for evaluating the health of saltmarshes. An understanding of the physiological and behavioral traits responsible for constraining the birds to that habitat may prove a valuable tool in understanding the processes that create and define saltmarshes.