SALT AND WATER BALANCE IN SEASIDE AND SHARP-TAILED SPARROWS

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THE aim of this study was to obtain data on drinking habits, capacities for concentrating urine, weight maintenance, and blood plasma regulation in the Sharp-tailed Sparrow (*Ammospiza caudacuta*) and the Seaside Sparrow (*A. maritima*) taken from different habitats and in different seasons.

I studied *A. maritima*, a salt-marsh species, *A. c. caudacuta*, which also breeds in salt marshes, and *A. c. subvirgata*, which breeds in brackish and freshwater habitats. I have compared these species with both fresh- and saltwater races of Song Sparrows (*Melospiza melodia*) and Savannah Sparrows (*Passerculus sandwichensis*). In these latter two species, differences have been demonstrated between salt- and freshwater forms in drinking habits and physiological capacities (Cade and Bartholomew, 1959; Poulson and Bartholomew, 1962; Bartholomew and Cade, 1963).

Seasonal differences in the environment exist in the area where the experimental birds were obtained. The birds must make more use of seeds and brackish water in their diet in the fall than in the spring; in the fall terrestrial arthropods are scarce and less fresh water is available from dew, coastal fog, and rain. Therefore, I compared the responses of fall-captured birds with those of birds caught in the spring.

METHODS

All birds were captured in mist nets on the sawgrass (*Spartina alternifora* and *S. patens*) and rush (*Juncus gerardi*) areas of the Great Island salt marsh in the mouth of the Connecticut River. Cardboard boxes were partly filled with rushes to avoid excess activity and injury to the birds while they were being transported to the laboratory.

The birds were kept in individual 25 × 25 × 48 cm cages in a windowless room and kept on a 12-hour photoperiod (lights on from 09:00 to 21:00), the temperature remained between 23° and 27°C, and the relative humidity between 43 and 64 per cent. For 1 to 2 weeks after capture the birds were fed mealworms (*Tenebrio*) as a supplement to chick mash and mixed bird seed; both the latter items consisted of 9 to 11 per cent water by weight. The mealworm supplement was necessary to prevent excessive mortality as *Ammospiza* normally depend heavily on insects and spiders for food (Woolfenden, 1956: 71). When the birds were started immediately on an exclusively dry diet with drinking water freely available, about 60 per cent ate poorly and died. Even with the supplement, a quarter of the birds died before they learned to eat and drink in captivity.

The eventual experimental population consisted of 9 spring- and 2 fall-caught *A. m. maritima* (stabilized laboratory weight, 19–24 g), 11 spring-caught *A. c. caudacuta* (14–17 g), 7 fall-caught *A. c. caudacuta* (13–16 g), 3 fall-caught *A. c. subvirgata* (17–19 g), and 3 fall-caught birds that appeared to be *A. c. subvirgata* × *A. c. caudacuta* intergrades because of intermediate weight (16–17 g) and plumage coloration

(Montagna, 1942). In addition, data were supplied by Charles Trost (See Figure 4 and RESULTS) on several individuals collected in Florida as follows: 1 each of *A. c. caudacuta*, *A. c. subvirgata*, and *A. c. nelsoni*, and 2 each of *A. m. maritima* and *A. m. nigrescens*. (Herein the Dusky Seaside Sparrow, *A. nigrescens*, is referred to as a race, *A. maritima nigrescens*, of the Seaside Sparrow (Griscom, 1944).)

Drinking devices, 100-ml graduates fitted with L-shaped drinking tubes, were used for a study of ad libitum drinking, minimum fluid requirements for weight maintenance, and salinity discrimination. A control tube was used to measure evaporation.

Ad libitum drinking was measured daily for at least 10 days and the same individuals were tested on each molarity (distilled water, 0.1, 0.15, 0.2, 0.3, 0.4, and 0.5) of NaCl. Starting the day after each such test, the minimum ration of the same molarity needed for weight maintenance was determined by progressively restricting the daily fluid ration until the bird could just maintain weight. Each morning, just after the lights came on, the birds were weighed to the nearest 0.1 g on a triple beam balance. The next day after minimum requirement of one molarity was determined, a bird was given the next more concentrated molarity ad libitum. Sometimes it took 1 or 2 days for the ad libitum drinking to reach a steady level; in such cases the stabilized ad libitum intake is reported. At the limits for weight maintenance, 0.4 or 0.5 M NaCl, the birds never reached a steady level so the average is presented.

The above procedure was used because it allows progressive acclimation of capacity to concentrate urine and thus measures the potential performance of each bird. The fall-caught *A. c. caudacuta* were not progressively acclimated (it was not evident at the time that fall-caught birds differ from spring-caught birds in ability to concentrate urine). Before being tested on the next more concentrated molarity the fall-caught *A. c. caudacuta* were permitted to drink distilled water ad libitum for 3 days. Such a procedure has been used in other studies similar to this but in most cases differences in results using this procedure and progressive acclimation have not been assessed using the same species.

Two to four fall-caught birds of each taxon were subjected to 3 days of complete water deprivation just after they had learned to eat and drink.

Relative drinking curves were constructed to facilitate comparison of ad libitum drinking by individuals that had been treated in different ways in the laboratory. The average amount of fluid drunk on each regimen (per cent body wt/day) was calculated and the maximum was assigned the value of 100; the average amounts of fluid drunk of all other molarities were then expressed as percentages of the maximum. Relative curves for minimum requirements were constructed in the same manner.

Activity, as measured by movements to and from a perch, was determined for two spring-caught individuals of *A. c. caudacuta* and two *A. m. maritima* for the last 5 days that they were drinking distilled water and 0.1, 0.2, and 0.3 M NaCl ad libitum. Activity was also measured for the two *A. c. caudacuta* while they were being restricted to the minimum ration of fluid needed for weight maintenance at each molarity. Relative activity curves were constructed to facilitate comparisons of activity by individuals that used their perches to different extents. The maximum amount of activity was assigned a value of 100 and activity on other regimens was expressed as a percentage of the maximum.

Blood and urine samples were taken from the birds after they had been drinking a solution ad libitum for at least 10 days. Blood samples of 20 μl or less were taken up into a heparinized capillary tube from the vein on the median side of the crus. Urine samples were taken up into disposable 5- or 10-μl capillary tubes from clean glass plates on the bottom on the bird's cage. First the glass plate was placed in the cage and covered. I then allowed at least half an hour for the bird to calm down before returning to the room, removing the paper over the glass plate, and collecting the first urine sample voided. Within 30 seconds after voiding the clearest portion of the cloacal excreta was picked up and sealed in the capillary tube with plasticene. The capillary tubes of blood or urine were centrifuged at 7,500 rpm for 10 minutes to sediment blood cells or uric acid and feces, respectively. Hematocrit and volume of clear urine were determined by measuring the relevant lengths in the capillary tube with vernier calipers.

Water samples from the marsh habitat and river at Great Island were taken to determine the salinity of water available to *Ammospiza*. I took 15 samples at high tide and 15 at low tide in October, the driest month of year, when the salinities were most likely to be maximal.

Chloride concentrations in plasma and urine and in water from the bird's habitat were determined with an Aminco-Cotlove automatic chloride titrator. Plasma osmolality was determined with a Ramsey-Brown micro melting-point apparatus.

A bird's ability to discriminate between distilled water and different molarities (0.1, 0.2, and 0.3) of NaCl was determined by choice experiments lasting at least a week. Distilled water was placed in one drinking device and the NaCl solution in an adjacent one. To minimize learning by the bird, the position of the distilled water was switched daily and the solutions were switched from one device to the other every 2 days. Three spring-caught *A. c. caudacuta* and four spring-caught *A. m. maritima* were used. The choice between distilled water and 0.3 M NaCl was tested after the birds had been drinking 0.3 M NaCl ad libitum. After a week the birds were switched to a choice between distilled water and 0.2 M NaCl and a week later to distilled water and 0.1 M NaCl.

Both *Ammospizas* and races of other salt-marsh sparrows were ranked according to parameters that affect salt and water balance (Table 5) so that rank correlation coefficients could be calculated. As Spearman rank correlation does not permit ties in ranking, it was necessary to make subjective evaluations in these cases. Two people independently evaluated ties; if they disagreed, rank was decided by a flip of a coin.

Seven parameters were ranked. Salinity of water available in a taxon's breeding and wintering habitat was ranked on the basis of chlorinities in the habitats. Maximum capacity to concentrate urine was ranked on the basis of direct measurements of urine/plasma ratios of osmolality or estimates thereof from the maximum molarity of NaCl drinking solution upon which body weight could be maintained. To correct for size differences between species, weight-relative ad libitum drinking and the minimum ration necessary for weight maintenance were ranked by departure from predictions based on expected ad libitum drinking and expected evaporative water loss, respectively (Figures 1 and 2, Bartholomew and Cade, 1963). As data on minimum requirements for weight maintenance are scarce, evaporative loss was used as a baseline for ranking minimum rations of salt-marsh birds. Response to acute dehydration was ranked by per cent daily weight loss for a 3-day period after withdrawal of a distilled water drinking solution. Finally two aspects of drinking response were ranked (Figure 3A, 3B). Figure 3A shows the scoring for rate of change of ad libitum intake with increasing salinity of the drinking solution and the relation of peak intake to maintenance of body weight. Figure 3B shows the scoring for the relationship between ad libitum intake and minimum ration necessary for weight maintenance when a bird is drinking distilled water and dilute salt solutions.

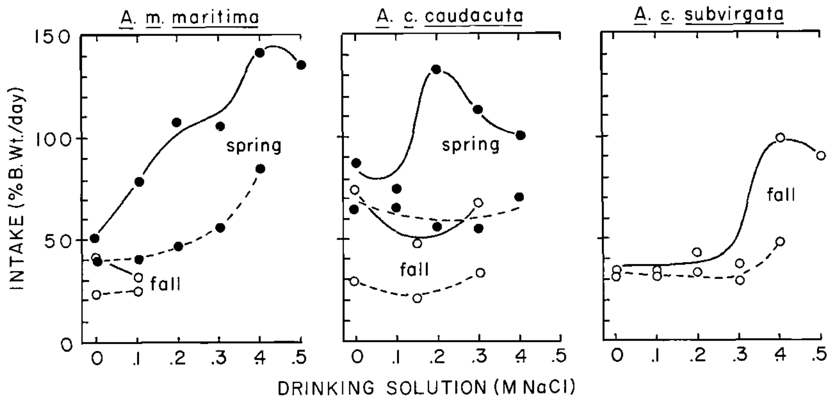

Figure 1. Water requirements for *Ammospiza.* Ad libitum drinking (solid lines) and minimum requirements for weight maintenance (broken lines) are shown for fall-caught (open circles) and spring-caught (closed circles) birds. Curves were fitted by eye.

RESULTS

RESPONSES OF BIRDS DRINKING AD LIBITUM

Ad libitum drinking.—Figure 1 and Table 1 show the relative amounts of water the birds drank on the different ad libitum regimens. None of these birds showed nocturnal water consumption. *A. c. caudacuta* drank more distilled water than *A. m. maritima* did in both spring and fall; both drank less distilled water in fall than in spring, but both drank more than *A. c. subvirgata* caught in fall. The amount that *A. m. maritima* drank in spring increased regularly with increased salinity, but in fall it drank less 0.1 M NaCl than distilled water. In contrast, ad libitum intake of dilute salt solutions by *A. c. caudacuta* was less than that of distilled water both in spring and fall. In contrast to both *A. c. maritima* and *A. c. caudacuta,* the amount that *A. c. subvirgata* drank of each salinity in fall remained constant until intake suddenly increased to its peak level when the birds drank 0.4 M NaCl. The *A. c. caudacuta* were unique in showing peak ad libitum intake while drinking a salinity much lower than the maximum that they tolerated.

The differences between the drinking curves shown in Figure 1, which represent combined data for all individuals of a taxon, are also generally seen in relative drinking curves for individual birds. This is important because it means that the composite curves are not some artifact of combining patterns that differ between individuals. Occasionally an individual displayed drinking responses of another taxon. For example, one *A. c. caudacuta* had a drinking curve typical of *A. c. subvirgata* and vice versa.

Activity.—The relative activity of spring-caught *A. m. maritima* and *A. c. caudacuta* was higher than for fall-caught *A. c. subvirgata* when all

TABLE 1
RELATIVE RATES OF DRINKING BY VARIOUS FORMS OF *AMMOSPIZA*[1]

Species, season, and (no. birds)		Drinking solution (M NaCl)						
		0.00	0.10	0.15	0.20	0.30	0.40	0.50
A. m. maritima								
spring (7)	ad lib.	52.0	78.2		108.2	105.0	142.8	136.3
		± 4.0	± 3.7		±29.6	±16.4	±33.1	±57.1
	min.	39.6	40.6		48.2	57.0	86.2	
		± 2.3	± 3.2		± 5.7	± 4.6	±15.2	
A. c. caudacuta	ad lib.	88.2,	74.4		133.7	113.0	100.6	
spring (5)		86.5	±15.7		±12.7	±18.1	±13.3	
	min.	65.3	65.8		56.2	54.9	71.7	
		± 3.7	± 7.4		± 4.4	± 2.5	± 4.5	
A. c. caudacuta	ad lib.	74.9		46.7		67.7		
fall (7)		± 8.7		± 9.3		± 8.0		
	min.	28.8		20.7		33.1		
		± 2.7		± 3.4		± 3.2		
A. c. subvirgata	ad lib.	33.0	33.8		43.4	35.8	98.4	91.0
fall (6)		± 3.5	± 5.4		± 3.4	± 4.1	±26.6	±30.7
	min.	34.0	32.9		34.3	27.9	47.8	
		± 5.0	± 3.6		± 3.8	± 6.2	±12.9	

[1] Expressed as mean per cent body weight per day ± SE of the mean. Data are for ad libitum drinking and minimum ration necessary for weight maintenance.

drank concentrated NaCl solutions. The birds in spring were captured after arrival on the breeding ground. Neither these birds nor the fall-caught *A. c. subvirgata* exhibited zugunruhe. The relative activity of *A. m. maritima* and *A. c. caudacuta* remained between 50 and 100 per cent when these birds were drinking distilled water and all NaCl solutions up to and including 0.4 M NaCl. Their activity dropped to between 25 and 60 per cent when they drank 0.5 M NaCl. In the case of the two *A. c. subvirgata*, the relative activity remained between 75 and 100 percent on molarities up to 0.3 M NaCl. On that regimen it dropped to between 30 and 75 per cent; it further decreased to about 25 per cent when the birds were provided with 0.4 M NaCl. As is usual in such measurements, 100 per cent activity for individuals of each taxon occurred when drinking 0.1 or 0.2 M NaCl as well as when drinking distilled water (Poulson and Bartholomew, 1962).

Weight maintenance.—Table 2 shows the changes in body weight while the birds were on different ad libitum regimens. Weight change per ml drunk was used as the measure of weight maintenance because it corrects for differences in body weight and differentiates between "nondrinkers" and "drinkers" at the maximum salinity on which a bird can maintain weight. Except for fall-caught *A. c. caudacuta* (which were not progressively acclimated, see METHODS), all the *Ammospiza* maintained

TABLE 2
Per Cent Change in Body Weight per ml Ad Libitum Fluid Intake by *Ammospiza*[1]

Species, season, and (no. birds)	Drinking solution (m NaCl)						
	0.00	0.10	0.15	0.20	0.30	0.40	0.50
A. m. maritima spring (7)	0.06 ± 0.018	0.12 ± 0.026		0.07 ± 0.018	0.03 ± 0.009	0.02 ± 0.009	−1.31 ± 0.616
A. c. caudacuta spring (5)	0.01 ± 0.004	0.12 ± 0.045		0.11 ± 0.015	0.01 ± 0.009	−0.17 ± 0.106	
A. c. caudacuta fall (7)	0.02 ± 0.014		0.03 ± 0.027		−0.03 ± 0.018		
A. c. subvirgata fall (6)	−0.01 ± 0.017	0.08 ± 0.43		0.02 ± 0.029	0.02 ± 0.026	−0.02 ± 0.023	−0.58 ± 0.397

[1] Values for a drinking regimen are expressed with respect to final weight on the previous regimen. Values cited are mean ± SE of the mean for drinking periods of 10 or more days.

TABLE 3

BLOOD PLASMA REGULATION AND HEMATOCRIT IN *AMMOSPIZA*[1]

Properties of blood	Drinking solution (M NaCl) 0.00	0.20	0.30	0.40	0.50
hematocrit (per cent)	52.7, 51.5	50.5 ± 0.13	47.3 ± 0.87	47.4 ± 1.15	49.6 ± 1.23
total osmolality (milliosmols)	345, 348	346 ± 1.6	355 ± 4.4	364 ± 4.3	383 ± 12.5
Chloride (mEq/l)	128, 124	125 ± 0.3	128 ± 1.4	126 ± 2.9	141 ± 4.0

[1] Values are expressed as mean ± SE of the mean. Taxa included are *A. m. maritima*, spring (3); *A. c. caudacuta*, spring (2); and *A. c. subvirgata*, fall (3). The data for distilled water include only one *A. m. maritima* and one *A. c. caudacuta*. Drinking solutions were provided ad libitum.

weight while drinking solutions as concentrated as 0.3 M NaCl. Spring-caught *A. c. caudacuta* lost weight when drinking 0.4 M NaCl even though they were no more active than and drank less fluid than *A. m. maritima* that slowly gained weight. All spring-caught *A. m. maritima* and fall-caught *A. c. subvirgata* lost weight rapidly while drinking 0.5 M NaCl whether they drastically reduced or greatly increased the amount of fluid drunk. This alternative drinking response accounts for the high standard error for weight maintenance of these forms at their limiting salinity. In contrast, spring-caught *A. c. caudacuta* showed a lower standard error for weight maintenance at their limiting salinity because they neither drastically reduced nor greatly increased their ad libitum drinking.

Rates of weight loss during acute dehydration were obtained for three fall-caught *A. c. caudacuta*, two *A. c. subvirgata*, and three *A. m. maritima*. The Sharp-tailed Sparrows lost a mean of 3.8 (3.0–4.9) per cent of their initial body weight per day and the Seaside Sparrows lost a mean of 2.9 (2.0–3.4) per cent per day.

Osmotic and ionic regulation.—Spring-caught *A. c. caudacuta* and *A. m. maritima* and fall-caught *A. c. subvirgata* showed complete overlap in hematocrit, plasma chloride concentration, and plasma osmolality while drinking NaCl solutions ad libitum. Consequently I combined the data for the three groups (Table 3). Hematocrit, plasma chloride concentration, and plasma osmolality became more variable as the molarity of the NaCl drinking solution increased. Mean chloride concentration did not rise until the birds drank 0.5 M NaCl. On the other hand mean osmolality increased slightly as the birds drank solutions more concentrated than 0.2 M NaCl; the greater increase of plasma osmolality in birds drinking 0.5 M NaCl can be accounted for by the increased plasma chloride concentration.

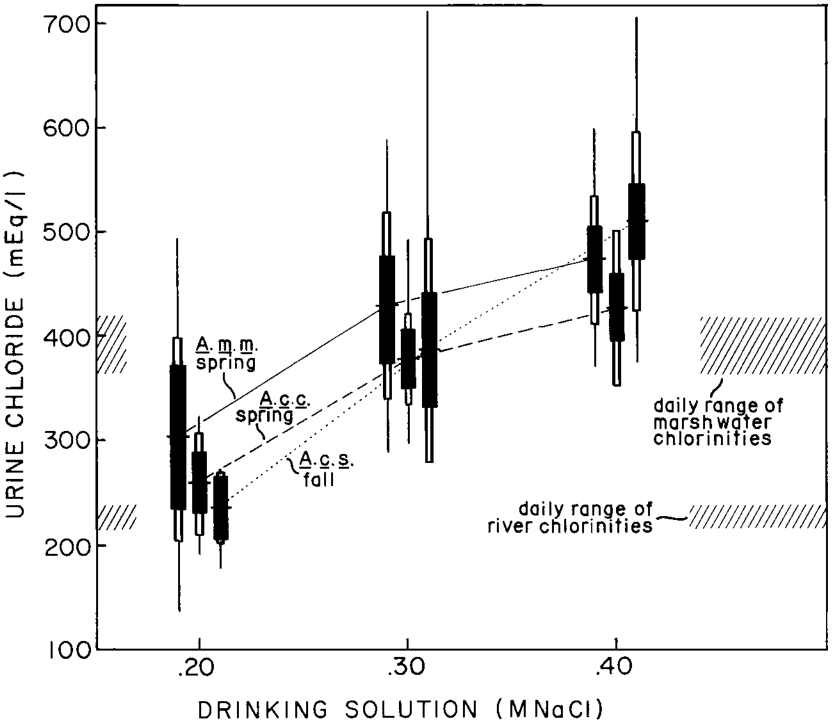

Figure 2. Capacity to concentrate urine in *Ammospiza*. Cloacal urine is compared to fall chlorinities of water available in the marsh where *A. m. maritima*, *A. c. caudacuta*, and *A. c. subvirgata* were collected. The symbolism used is: mean, horizontal line; mean ± 2 SE of the mean, black bar; mean ± 1 SD, white bar; and range, vertical line.

Birds progressively acclimated to increasingly concentrated NaCl drinking solutions were able to excrete cloacal urine with mean chloride concentrations equal to or higher than the maximum chlorinities of water available to them in their salt-marsh habitat (Figure 2). The urine of spring-caught *A. m. maritima* was consistently more concentrated than that of spring-caught *A. c. caudacuta* by about 45 mEq Cl^-/l but this difference is not significant at the 95 per cent level. The urine chloride concentration of fall-caught *A. c. subvirgata* drinking 0.4 M NaCl is significantly higher than that of spring-caught *A. c. caudacuta* at the 95 per cent level.

In October, when salinity is likely to be maximal, the salinity of the water available to the birds at Great Island was lowest in the river at the edge of the marsh and highest around the drainage ditches in the center of the marsh. At low tide the chloride concentrations in the river averaged

TABLE 4

SALINITY DISCRIMINATION BY INDIVIDUAL *AMMOSPIZA*[1]

	Choice Combinations								
	0 vs. 0.1 M NaCl			0 vs. 0.2 M NaCl			0 vs. 0.3 M NaCl		
		Intake % body wt/day			Intake % body wt/day			Intake % body wt/day	
Species	Ratio 0/0.1	NaCl	Fluid	Ratio 0/0.2	NaCl	Fluid	Ratio 0/0.3	NaCl	Fluid
A. c. caudacuta	2.5	.11	61	6.1	.16	93	6.5	.26	101
	2.0	.28	144	2.2	.38	106	7.5	.22	151
	2.0	.25	130	3.5	.17	116	—	—	—
mean	2.2	.21	112	3.9	.24	105	7.0	.24	126
A. m. maritima	−2.0	.25	109	7.9	.12	91	4.8	.24	132
	6.6	.08	108	3.0	.19	68	3.1	.33	125
	1.5	.11	48	−1.5	.25	39	2.2	.30	54
	2.1	.16	100	2.1	.28	82	—	—	—
mean	2.1	.16	91	2.9	.21	70	3.4	.29	104

[1] Birds were given the choice between distilled water and dilute NaCl solutions.

217 mEq/l (210–231) and on the marsh 365 mEq/l (352–391). At high tide the concentrations in the river averaged 239 mEq/l (235–243) and on the marsh 410 mEq/l (374–443). In the spring rain is more prevalent along the Connecticut shore and lowers the salinity of the coastal waters. Dew and fog also are available when they condense on plants.

Salinity discrimination.—Given a choice between distilled water and dilute solutions of NaCl, spring-caught *A. c. caudacuta* and *A. m. maritima* discriminated against the salt solution to the same degree and had similar weight-relative salt ingestion (Table 4). The only exception was that *A. c. caudacuta* showed stronger discrimination against 0.3 M NaCl than did *A. m. maritima.* On the average the birds tested showed slight increases in salt ingestion with increased salinity of the solutions offered, even though their discrimination against the salt solution increased.

RESPONSES TO RESTRICTION OF WATER

Minimum needs for weight maintenance.—Table 1 and Figure 1 show the minimum rations of various NaCl solutions needed to maintain weight. Except for fall-caught *A. c. subvirgata,* minimum needs were lower and less variable than ad libitum intake on all regimes tested. In contrast to ad libitum intake, minimum needs of *A. c. caudacuta* and *A. m. maritima* remained about the same or increased gradually as the salinity of the drinking solution increased. As was the case for ad libitum drinking, minimum needs of *A. c. caudacuta* and *A. m. maritima* were lower in the fall than in the spring.

Activity during restriction of water.—For dilute salt solutions, 0.1 and 0.2 M NaCl, the relative and absolute amount of activity of the two *A. c. caudacuta* tested was no lower when the birds were restricted to minimum rations than it was when they drank those fluids ad libitum. When drinking more concentrated solutions the birds were much less active when restricted to minimum rations than they were when drinking ad libitum.

DISCUSSION

AD LIBITUM DRINKING

Distilled water.—Salt-marsh passerine birds drink more distilled water than birds of the same weight from other mesic habitats. In their review Bartholomew and Cade (1963) illustrate this response (pattern C) with data on two races of *Passerculus sandwichensis* and two races of *Melospiza melodia.* These salt-marsh races drink 1.5 to 6.0 times as much as do nonsalt-marsh birds of similar weights (Figure 2 in Bartholomew and Cade, 1963). To exemplify this pattern further, Table 5 presents data for four additional salt-marsh taxa, two races of *Ammospiza maritima* and two of *A. caudacuta.*

The weight-relative amount of distilled water salt-marsh passerines

TABLE 5

RANKING OF PARAMETERS RELATED TO SALT AND WATER BALANCE FOR SALT-MARSH BIRDS AND THEIR RELATIVES[1]

Taxon	Salinity rank	Salinity chlorinity	Urine conc rank	Urine conc U/P	Drinking dist. H_2O observed—expected: Ad libitum rank	Ad libitum % B.wt/d	Drinking dist. H_2O observed—expected: Minimum rank	Minimum % B.wt/d	Weight maint. rate of change of drinking rank (Figure 3A)	Ad lib. intake relative to minimum need rank (Figure 3B)	Weight loss during acute dehydration rank	Weight loss % B.wt/d
Melospiza melodia cooperi	1	2			1	- 4						
Passerculus s. sandwichensis	2	4	4	3.3	2	- 3	1	+ 3	2		4	-3.2
Ammospiza caudacuta nelsoni	3	10	2	2.6	3	+ 3			1			
P. s. brooksi	4	12	1	2.2	5	+14	4	+14	3	1	3	-3.3
A. c. subvirgata	5	15	3	2.9	4	+ 7	5	+16	4	2	2	-3.6
M. m. maxillaris	6	17			6	+15						
A. m. maritima	7	23	6	3.5	7	+18	2	+ 8	5	3	6	-2.9
A. c. caudacuta	8	24	5	3.4	9	+47	3	+11	6	4	1	**-3.8**
M. m. samuelis	9	25			8	+23						
P. s. beldingi	10	35	7	4.5	10	+75	6	+30	7	5	5	-3.0

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[1] Except for the drinking data for *Melospiza* and *A. c. nelsoni* (see DISCUSSION), all data were gathered by the author. The data on *A. m. nigrescens* were consistent with those for *A. m. maritima.*

drink is related to the salinity of water available in their wintering and breeding habitats. Departure of ad libitum intake from that expected for species of the same weight from nonsalt-marsh habitats shows a highly significant correlation ($P < 0.01$) with salinity of available water. Fall drinking data were used in computing the overall species correlation because at that season *Ammospiza* has a largely granivorous diet like that of the other species used. In spring the diet of *Ammospiza* includes many insects.

The dependence of ad libitum drinking on available salinity holds within species as well as between species. The rank orders of salinity and ad libitum drinking, regardless of season, are the same within *Passerculus sandwichensis*, *Melospiza melodia*, and *Ammospiza caudacuta*. In each case one of the three races of each species tested occurs in nonsalt-marsh habitats and its ad libitum intake is close to that expected for species of similar weight that are not from salt marshes (Table 5).

Regulation of salt ingestion.—The high level of salt ingestion by salt-marsh passerines in a choice situation is due to their high ad libitum drinking and not to a unique pattern of salinity discrimination. When given a choice between distilled water and 0.1 M NaCl, *A. c. caudacuta* and *A. m. maritima* do not differ from nonsalt-marsh forms in their discrimination against the salt solution (Table 4 and Bartholomew and Cade, 1963). Salt-marsh forms survive on higher salinities than do nonsalt-marsh inhabitants, but both tend to regulate their levels of salt ingestion at some constant level that is roughly correlated with their level of ad libitum drinking: e.g. *A. c. caudacuta* regulates its NaCl ingestion at 0.21–0.24 per cent body wt/day while drinking between 105 and 125 per cent body wt/day, whereas the nonsalt-marsh *Carpodacus mexicanus* ingests 0.03–0.08 per cent body wt/day of NaCl while drinking 22–40 per cent body wt/day. Despite regulation of salt ingestion at a population level (Table 4), individual *Ammospiza* do not appear to regulate their salt intake at a constant level. Data are not available to show whether individuals of other species so regulate their intake or not.

Drinking of distilled water and dilute salt solutions.—Salt-marsh passerines show lower ad libitum drinking of dilute salt solutions than of distilled water or moderately concentrated salt solutions and the same or lower minimum requirements for weight maintenance. The development of this drinking response (scored as indicated in Figure 3B) is significantly correlated ($P < 0.01$) with the salinity of water available in the wintering and breeding habitats of salt-marsh passerines. A parallel response is seen when salt-marsh *Ammospiza* are given a choice between distilled water and dilute salt solutions. Individuals of *A. c. caudacuta* and *A. m. maritima* drink less total fluid when given a choice between distilled

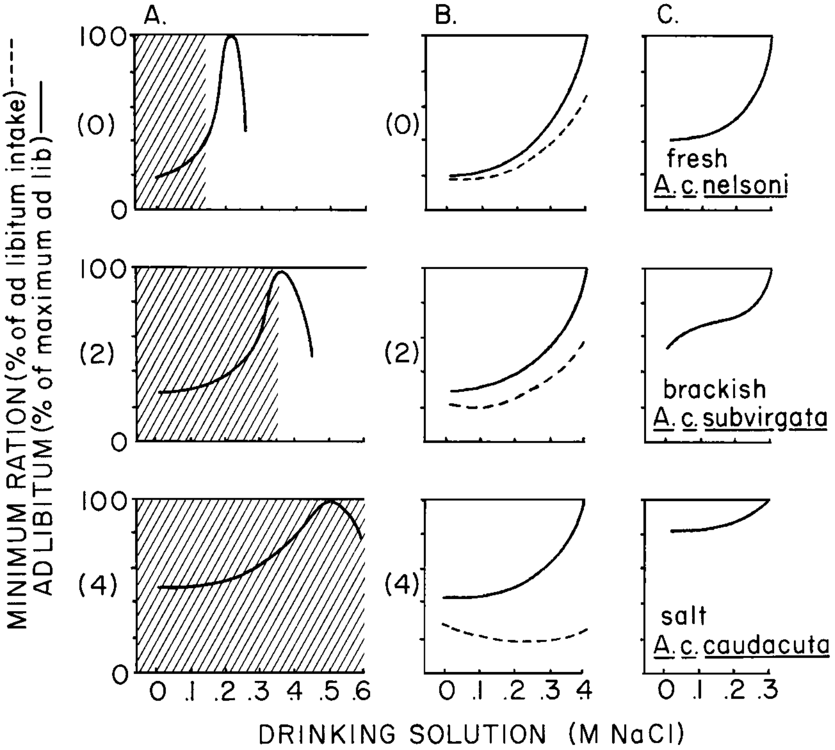

Figure 3. Relative drinking curves for salt-marsh passerines. Graphs under A show the relation between weight maintenance (hatched area) and rate of change of steady state ad libitum drinking. Under B is the relation between ad libitum drinking and minimum requirement for weight maintenance. Scoring for A and B, from 0 to 4, was used to rank the drinking curves for each taxon (Table 5). Graphs under C (data supplied by C. Trost) are for *Ammospiza caudacuta* which are exposed to different salinities in their natural habitats.

water and 0.2 M NaCl than when given a choice between distilled water and either 0.1 or 0.3 M NaCl (Table 4). This drinking response of salt-marsh passerines, as well as the high ad libitum drinking of distilled water, remains to be explained. It is not likely due to overcompensation in drinking dilute solutions in an attempt to replace excreted ions, as the salt-marsh Savannah Sparrow *P. s. beldingi* shows no higher urine chloride than the freshwater *P. s. brooksi* when both drink distilled water ad libitum (Poulson and Bartholomew, 1962).

Drinking of salt solutions and weight maintenance.—A drinking response characterized by a slow increase in amount drunk of increasingly saline solutions and the peak intake on a salinity below the maximum concentration on which body weight is maintained (Figure 3A, bottom) is adaptive in salt marshes. Such drinking responses, as shown by *A. c. caudacuta*, are typical of salt-marsh forms and probably enable them to exploit temporarily drinking sources more concentrated than their limiting salinity for weight maintenance, and also to survive long enough to acclimate. In other words, the drinking response of salt-marsh birds reinforces their maximum potential for urine concentration, whereas the response shown by nonsalt-marsh birds does not permit them to achieve their maximum potential for urine concentration. Spring-caught *A. c. caudacuta* have a lower capacity to concentrate their urine than fall-caught *A. c. subvirgata* (Figure 2), but the salt-marsh *A. c. caudacuta* has the same limiting salinity as the brackish-marsh breeder *A. c. subvirgata* because the drinking response of *A. c. caudacuta* reinforces its capacity to concentrate its urine.

In contrast to the drinking response shown by salt-marsh passerines, nonsalt-marsh passerines increase their stabilized ad libitum intake almost logarithmically as they are given more concentrated saline solutions to drink (pattern A in Bartholomew and Cade, 1963), and their peak intake is of concentrations higher than those on which they can maintain their body weight (Figure 3A, top). If the only salinity available is one close to the concentration for peak ad libitum drinking, a nonsalt-marsh passerine will show one of two responses, both of them fatal. One response is a high initial rate of drinking, in which case blood osmolality increases fast enough to inhibit activity, drinking, and feeding. The alternate response is a slower initial rate of drinking. Salt intake is still sufficient to induce diuresis, and the urine is not enough more concentrated than the drinking solution to balance the salt intake and leave enough osmotically unobligated water to compensate for evaporative water loss. The result is a slow increase in blood osmolality and further stimulation of drinking, i.e. a positive feedback. These alternate responses to saline waters explain the great variability of weight loss and drinking for nonsalt-marsh birds exposed to salinities at or near their limit for weight maintenance. A comparison between the brackish-marsh *A. c. subvirgata* and the salt-marsh *A. c. caudacuta* illustrates this point (Tables 1 and 2).

CAPACITY TO CONCENTRATE URINE

For those forms on which direct measurements of urine/plasma ratios were not available, capacity to concentrate urine was estimated from the maximum molarity of NaCl on which they maintained weight while drinking ad libitum (Table 5). This maximum molarity is significantly correlated with maximum urine/plasma ratio ($P < 0.01$).

Urine concentration and salinity of drinking water.—The correlation between maximum capacity to concentrate urine and the salinity of water available in the breeding and wintering habitats is highly significant ($P < 0.01$). This is consistent with the supposition that salt-marsh passerines obtain a major portion of their free water by drinking saline water in their natural habitats.

Seasonal changes.—Indirect evidence suggests that *A. m. maritima* and *A. c. caudacuta* have a greater capacity to concentrate their urine in fall than in spring (Figure 1). First, birds given only a dry diet have a lower ad libitum intake of distilled water when caught in the fall than when caught in spring. Second, collection of birds after establishment of territories in spring precludes an effect of zugunruhe. Third, in fall *Ammospiza* show a slower increase in stabilized ad libitum drinking with increasing salinity of their drinking solution than they show in spring. The development of this drinking response (Figure 3A) is significantly correlated with capacity to concentrate urine ($P < 0.01$).

A seasonal change in capacity to concentrate urine would be adaptive for *Ammospiza* because of seasonal changes in sources of free water. In fall water is less available as dew, coastal fog, rain, green nonhalophytic plants, and insects. The diet of *Ammospiza* must include more seeds, and the birds must rely on the saline water in their habitat more than they do in spring and summer. During migration the low salinity waters of estuaries are not always available.

THE MEANING OF AD LIBITUM DRINKING AND MINIMUM REQUIREMENT

Two lines of evidence suggest that ad libitum drinking and minimum requirements of water for weight maintenance of salt-marsh passerines and their relatives may be indices of the development of different mechanisms of water conservation. First, the correlation between departures of ad libitum drinking and minimum requirements of distilled water from values predicted on the basis of data for nonsalt-marsh passerines (Figures 1 and 2 in Bartholomew and Cade, 1963) is not significant (P 0.18). Some data on *Ammospiza* show why this correlation is poor. Both *A. m. maritima* and *A. c. caudacuta* show the same difference between spring and fall ad libitum drinking, but the difference between spring and fall minimum requirements for *A. c. caudacuta* is more than twice that for *A. m. maritima* (Figure 1). Also the spring data for *A. m. maritima* show that minimum requirements can be nearly the same for distilled water 0.1 and 0.2 M NaCl, whereas stabilized ad libitum intake increases regularly for 0.1 and 0.2 M NaCl regimes.

The second line of evidence is that ad libitum drinking is reasonably well correlated with capacity to concentrate urine and poorly correlated with rate of weight loss during acute water deprivation (P 0.03 and 0.30). The good correlation of ad libitum drinking with capacity to concentrate urine may be secondarily due to both being highly correlated with the salinity of water available in the habitat. On the other hand minimum requirements are poorly correlated with capacity to concentrate urine and reasonably well correlated with rate of weight loss during acute dehydration (P 0.27 and 0.07).

From the data on *Ammospiza*, differentially high ad libitum intake of distilled water by salt-marsh passerines is apparently not due to a differential requirement for salt. The two salt-marsh species of *Ammospiza* have similar ad libitum ingestions of NaCl when given a choice between distilled water and dilute NaCl solutions, even though they differ by twofold in total ad libitum fluid intake (Table 4), and the level of ad libitum drinking for each species given only distilled water was the same as when each was given the choice between distilled water and 0.1 M NaCl.

For salt-marsh passerines minimum requirement for weight maintenance is a more meaningful ecological index of tolerance to dehydration than is rate of weight loss during acute deprivation of water. Data on *A. c. caudacuta* show that determination of minimum requirement by progressive restriction of water ration is not accompanied by a decrease in activity or feeding. On the other hand, nondesert passerines show decreased activity and feeding when subjected to acute deprivation of water (Smyth and Bartholomew, 1966). This difference is reflected by the lack of great inter- and intraspecific differences in rate of weight loss during acute dehydration for salt-marsh passerines that have very different minimum requirements for weight maintenance (Table 5).

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SUMMARY

One race of Seaside Sparrow, *Ammospiza maritima maritima*, and two races of Sharp-tailed Sparrow, *Ammospiza caudacuta caudacuta* and *A. c. subvirgata*, drinking distilled water and 0.10 to 0.50 M NaCl, showed capacities to concentrate urine and drinking responses that were significantly correlated with the salinity of water available in each race's habitat. In subspecies exposed to full seawater in their natural habitats, e.g. *A. c. caudacuta*: 1. Maximum capacity to concentrate urine was great. 2. Peak ad libitum drinking occurred when a bird was exposed to NaCl solutions less concentrated than the maximum salinity on which it could maintain weight and then it drank less and less of concentrations greater than its

peak intake. 3. Ad libitum drinking of distilled water was very high. 4. The greatest difference between ad libitum intake and minimum requirement for weight maintenance was seen when a bird drank NaCl solutions intermediate in concentration between distilled water and the maximum on which weight was maintained. These four patterns were reviewed for other salt-marsh passerines and their adaptive value discussed.

When both distilled water and dilute NaCl solutions were available in a choice situation, individual *A. m. maritima* and *A. c. caudacuta* showed great variability in salt ingestion, but the average levels of salt ingestion for distilled water vs. 0.1, 0.2, and 0.3 M NaCl were relatively constant. The level of salt ingestion for these salt-marsh passerines was compared to that for nonsalt-marsh forms.

The *A. c. caudacuta* and *A. m. maritima* caught in spring and the *A. c. subvirgata* caught in fall showed similar capacities to regulate their hematological properties while drinking ad libitum. Hematocrit and both osmolality and [Cl^-] of the plasma became more variable as the birds drank solutions more concentrated than 0.2 M NaCl, but average values did not increase significantly until they drank 0.5 M NaCl.

While drinking 0.4 M NaCl ad libitum, after progressive acclimation drinking 0.1, 0.2, and 0.3 M NaCl, the *A. c. caudacuta* and *A. m. maritima* caught in spring and the *A. c. subvirgata* caught in fall regularly produced cloacal urine with concentrations of 450 mEq $Cl^-/1$, a concentration 3.5 times that of their blood plasma and slightly more than the maximum for the brackish water available where the birds were collected.

During restriction to minimum requirements of distilled water and 0.1 and 0.2 M NaCl, *A. c. caudacuta* maintained the same level of activity as when drinking distilled water ad libitum.

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