

SALT WATER TOLERANCE AND THE DISTRIBUTION OF SOUTH SAN FRANCISCO BAY SONG SPARROWS¹

MICHAEL P. BASHAM² AND L. RICHARD MEWALDT

Avian Biology Laboratory, San Jose State University, San Jose, CA 95192

Abstract. The Alameda Song Sparrow (*Melospiza melodia pusillula*) inhabits the salt marshes surrounding south San Francisco Bay. The Marin Song Sparrow (*M. m. gouldii*) resides in upland riparian habitats surrounding the entire bay system. To determine the effects that drinking water salinity might have on subspecies distribution, increasing proportions of seawater and NaCl in drinking solutions were tested using 22 individuals of each race. *M. m. pusillula* maintained body weight more effectively on concentrated drinking solutions than did *M. m. gouldii*. *M. m. pusillula* also showed a greater tolerance of weight loss than did *M. m. gouldii*. *M. m. pusillula* showed an ad libitum freshwater consumption typical of other salt-marsh fringillids and increased its consumption only slightly as the concentration of the drinking solution rose. *M. m. gouldii* showed a high level of ad libitum freshwater consumption and increased its fluid intake greatly as the drinking solution became more saline. Both races were able to maintain body weight on solutions as concentrated as those found in their respective habitats. *M. m. gouldii* was unable to maintain weight on water as saline as that found in local salt marshes. This may confine its distribution to upland regions which would tend to limit gene flow between populations of these two races. On the margins of south San Francisco Bay, habitat alteration and fragmentation may be altering distribution of the two races.

Key words: Song Sparrow; *Melospiza melodia*; salt tolerance; subspecies distribution; San Francisco Bay.

INTRODUCTION

The Alameda Song Sparrow (*Melospiza melodia pusillula*), henceforth referred to as *pusillula*, is a permanent resident of the salt marshes surrounding the southern arm of San Francisco Bay (Johnston 1968) (Fig. 1). Although this habitat is mesic, free standing fresh water or dew are not dependably available especially during the warmer six months of the year. The Marin Song Sparrow (*M. m. gouldii*), henceforth referred to as *gouldii*, is an upland form residing in riparian and other moist, freshwater habitats surrounding San Francisco Bay. It is the most widespread of the four races of San Francisco Bay area Song Sparrows (Walton 1978).

Typically, populations of resident Song Sparrows are highly sedentary and rarely venture more than 10 m from cover (Nice 1937, Marshall 1948a, Johnston 1956a, Halliburton and Mewaldt 1976). Consistent with this sedentary nature, there is no evidence that individuals of *pusillula* fly the 1 to 5 km or more to available

sources of fresh water when none is available in their habitat. To determine the comparative abilities of *pusillula* and *gouldii* to tolerate saline drinking water was the objective of this study.

Three salt-marsh races *M. m. pusillula*, *M. m. samuelis*, and *M. m. maxillaris* occupy and are almost entirely limited to the salt and brackish marshes of greater San Francisco Bay and the Sacramento-San Joaquin Delta. In contrast, *gouldii* occupies suitable upland habitats completely surrounding the three salt-marsh races. The four races are morphologically distinct and show certain habitat preferences. Their sedentary natures and generally short juvenile dispersal distances keep them geographically isolated and thus limit genetic contact (Marshall 1948a, 1948b; Johnston 1956a, 1956b; Halliburton and Mewaldt 1976). Since late in the 19th century, the fragmentation of their original habitats with salt evaporators, harbors, dumps, subdivisions, highways, etc. has further limited genetic contact among the races (Walton 1978).

Passerine birds are not known to have nasal salt glands such as are possessed by many marine birds (Peaker and Linzell 1975). Thus, from a physiological standpoint their water/salt balance may come under strain when fresh water is not

¹ Received 10 February 1986. Final acceptance 16 March 1987.

² Science Department, El Dorado High School, 561 Canal Street, Placerville, CA 95667.

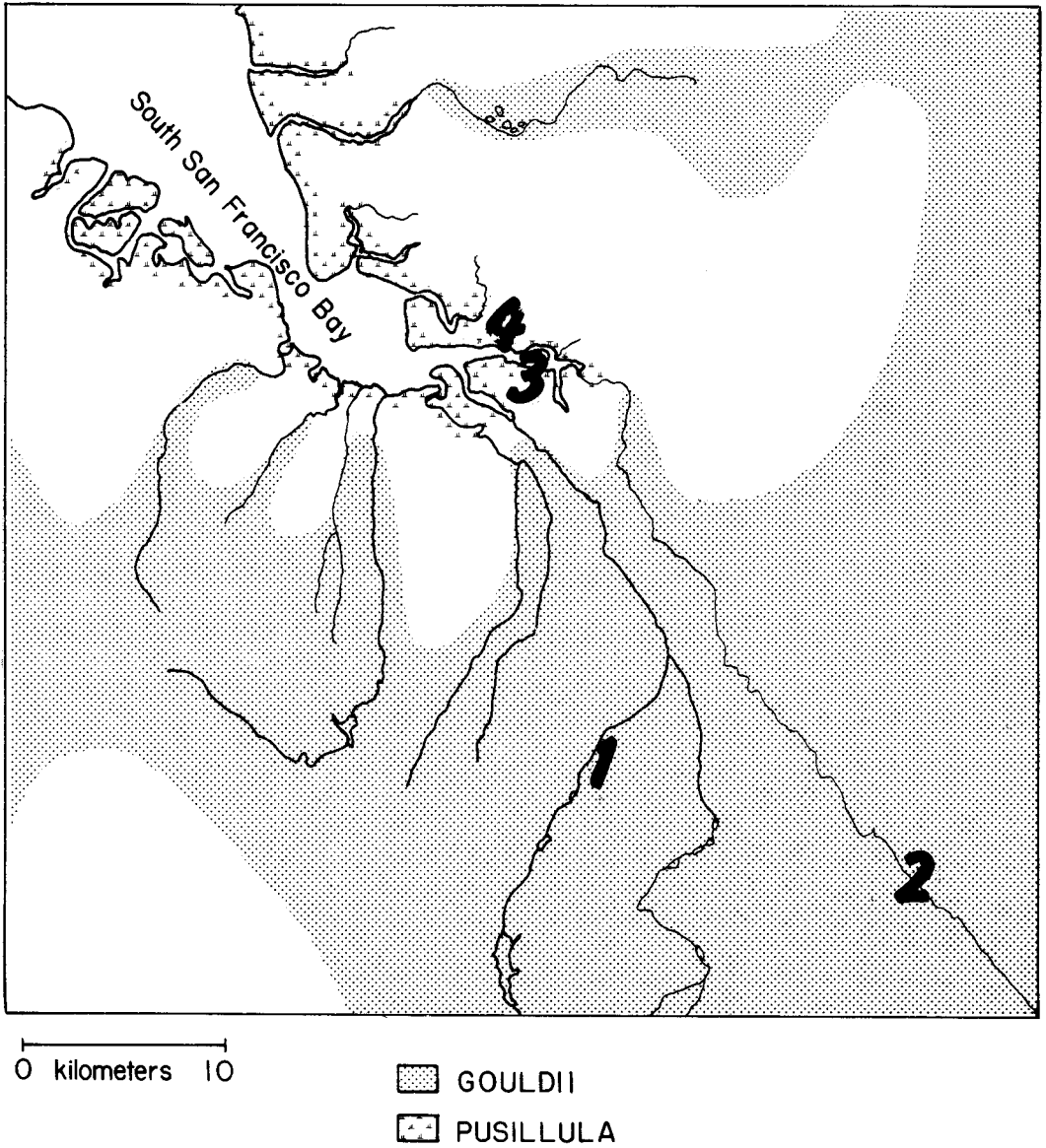


FIGURE 1. Distribution of Song Sparrow populations of the South San Francisco Bay region (adapted from Marshall 1948a and Walton 1978). Numbers show capture locations as follows: (1) Los Gatos Creek, (2) Coyote Creek, (3) Triangle Marsh, and (4) Aubry Slough.

available. Studies on salt-marsh Savannah Sparrows (*Passerculus sandwichensis beldingi* and *P. s. rostratus*) showed that they were able to maintain body weight on saline solutions more effectively than migratory populations (*P. s. nevadensis* and *P. s. brooksi*) which presumably breed in freshwater habitats (Cade and Bartholomew 1959; Poulson and Bartholomew 1962b). These salt-marsh races were able to maintain body

weight on 100% seawater and on 0.6 M NaCl. Preliminary studies were also conducted on two races of salt-marsh Song Sparrows from the northern San Francisco Bay region (*M. m. samuelis* and *M. m. maxillaris*) (Bartholomew and Cade 1963). It was found that these birds could maintain body weight effectively on seawater concentrations only up to 50% (Cade, pers. comm.). The *pusillula* we used live in the south-

ern reaches of San Francisco Bay where salinities can range from 0.109 M Cl⁻ in winter to 0.367 M Cl⁻ in summer (Table 1). These salinities are greater than those further north (San Pablo Bay) and the delta (Suisun Bay) where the other two races live (Marshall 1948a). Thus, *pusillula* faces an environment that is more stressful, osmotically, than the other two salt-marsh races.

Are there differences in the physiological responses in Song Sparrows of the salt-marsh race *pusillula* and the upland race *gouldii* to fresh and saline drinking water? Do these represent adaptations to selective pressures in the contrasting availability of fresh water in salt-marsh and upland habitats? Is *pusillula* better adapted to live in salt-marsh habitats than *gouldii*?

METHODS

The 22 individuals of each of *pusillula* and *gouldii* were captured in the winter of 1979 and summer of 1980 using mist nets (Basham 1983). Individuals of *pusillula* were taken in the salt marshes near Alviso, California within the San Francisco Bay National Wildlife Refuge. Individuals of *gouldii* were taken at various locations along Los Gatos Creek, near Los Gatos and Coyote Creek, near Coyote (Fig. 1). All birds were banded with numbered, aluminum leg bands and transported to San Jose State University, San Jose, California. During acclimation the birds were placed two per cage in one of two environmental chambers maintained continuously under conditions of 12L:12D photoperiod (mean light intensity of 2,820 lux, range 1,730–3,620 lux) with temperature and relative humidity at 20°C and 50%, respectively. Tap water from 12 mm × 160 mm stainless steel, rodent drinking tubes bent to an angle of 68° and ground Purina Dog Chow were available ad libitum. The birds were maintained in this manner until 31 July 1980. On 1 August 1980 all birds were transferred to individual cages placed alternately by race, and randomly within each race, along the counter-tops in each of the two rooms and maintained under the above conditions for 30 days prior to the beginning of the actual experiment. Paper liners, which were changed every other day, were placed in the bottom of each cage.

TAP WATER AND SEAWATER REGIMENS

The birds were maintained successfully for periods of 12 to 14 days on drinking solutions of:

tap water, 25% seawater, 50% seawater, and 60% seawater. The stainless steel drinking tubes, mounted in single-hole rubber stoppers, were placed in 100-ml graduated cylinders. The fluid-filled cylinders were mounted upside down on ring stands so that the consumption could be read directly from the graduations on the cylinders. The device was placed adjacent to the rear of the cage, with the drinking tip of the tube itself located just outside the cage. To drink, the birds had to extend their bills between the bars of the cage to the tip of the tube. In this way spilling due to cage vibration was eliminated. The water volume was recorded daily to the nearest 0.25 ml immediately prior to the end of the photoperiod. A control water device was placed in each room to correct for evaporation. The 12-hr light period began at 04:00. Following 12L, which ended at 16:00, was a 1-hr dim twilight period (mean light intensity 2.10 lux, range 0.5–4.9 lux) during which the cages were serviced and the birds weighed. The birds were weighed daily at the beginning of each regimen when rapid weight loss was possible and on alternate days once the body weight of individual birds became somewhat stabilized. Body weight was recorded to the nearest 0.1 g using an electronic top loading, single pan balance.

The birds were continued on each regimen until acute dehydration was noticed. Typically dehydrated birds had usually stopped drinking during the previous 24 hr and showed substantial weight loss (often greater than 20% initial body weight in 48 hr), were inactive, usually fluffed their plumage, and blinked their eyes more than usual. These birds were judged to have failed on that fluid regimen and were allowed to rehydrate on distilled or tap water. Most of these revived birds were used in subsequent experiments, and were ultimately rebanded with U.S. Fish and Wildlife Service bands and released at their capture sites.

Seawater (0.54 M NaCl) was obtained from the seawater aquarium facility at San Jose State University. It was transported on a regular basis from Moss Landing Marine Laboratories on the central coast at Moss Landing, California. The water was filtered mechanically and exposed to ultraviolet radiation. The seawater solutions were mixed by volume using fresh seawater and distilled water. Each batch was titrated with silver nitrate and potassium dichromate to determine chloride molarity (A.P.H.A. 1976).

TABLE 1. Water salinities at capture sites of San Francisco (S F) Bay (salt marsh) and Coyote Creek (riparian) Song Sparrows.

Location	Season	Tide	Molarity Cl ⁻	Range	SE	n
S F Bay	summer	low	0.273	0.155-0.367	0.010	22
S F Bay	summer	high	0.252	0.212-0.324	0.040	14
S F Bay	winter	low	0.204	0.195-0.208	0.005	4
S F Bay	winter	high	0.147	0.109-0.185	0.003	2
Coyote Creek	summer	—	0.007	0.000-0.014	0.007	2

DISTILLED AND NaCl REGIMENS

Using a modification of the above procedure the birds were retested on a series of distilled water and NaCl regimens in which the NaCl concentrations were increased far more gradually. The birds were maintained 12 to 14 days on each of the following regimens: distilled water, 0.11 M, 0.16 M, 0.22 M (21 days), 0.27 M, 0.32 M, 0.38 M, and 0.43 M NaCl. These solutions correspond to 0%, 20%, 30%, 40%, 50%, 60%, 70%, and 80% seawater in terms of chloride molarity. Each solution was made by weighing out the appropriate amount of NaCl and adding distilled water. Samples from all solutions were titrated to determine chloride molarity (A.P.H.A. 1976). Room conditions were the same as for the seawater tests. Water consumption and body weight data were also collected according to the same plan.

TABLE 2. Tolerance of salt-marsh and upland Song Sparrows to increasing salinity of drinking water.

Drinking solution	<i>M. m. pusillula</i>			<i>M. m. gouldii</i>		
	No. tested	No. tolerant	% tolerant	No. tested	No. tolerant	% tolerant
% seawater						
0	22	22	100	22	22	100
25	22	20	91	22	22	100
50	21	6	29	22	6	27
60	6	2	33	6	0	0
70	2	0	0	0	—	—
Molarity NaCl						
0.00	15	15	100	16	16	100
0.11	18	18	100	18	18	100
0.16	18	18	100	18	18	100
0.22	18	18	100	18	18	100
0.27	18	18	100	18	17	94
0.32	18	15	83	17	6	35
0.38	15	7	47	6	0	0
0.43	7	1	14	0	—	—

SALINITY OF WATER IN HABITAT

Table 1 shows the mean chloride concentrations of the water during summer and winter at the salt-marsh capture sites of *pusillula*. Collections were made at both high and low tide during the same 12-hr period. Chlorinity was also monitored in the freshwater riparian habitat (Coyote Creek) where *gouldii* were captured. The greater chlorinities in the salt marshes at low tide, than at high tide can be explained by evaporation that occurs. We found the salinity of water in shallow pools, remaining at low tide, increased prior to the entire marsh being inundated at high tide. The data in Table 1 also show that chlorinity is higher in summer than in winter when these marshes are often saturated with heavy rains. The range in salinities, especially in summer (Table 1) reflect differing conditions between salt marshes as well as between sites on the same marsh.

RESULTS

RESPONSES TO SEAWATER DRINKING SOLUTIONS

Numbers of *pusillula* and *gouldii* which tolerated our initial tests with increasing percentages of seawater were similar (Table 2). On 50% seawater neither race seemed very tolerant as only six of each subspecies completed the regimen. None of the *gouldii* and only two *pusillula* could tolerate 60% seawater. No individual of either race was tolerant of 70% seawater.

When fluid consumption values for increasing percentages of seawater in their drinking solutions were examined, we saw that *pusillula* and *gouldii* responded differently. *Pusillula's* ad libitum fluid consumption (as percent body weight per day) was generally less than that of *gouldii* (Fig. 2), but the difference was significant only on the 50% seawater regimen. Two trends are apparent. First, as the seawater concentration was

increased, *gouldii* increased its fluid consumption. Secondly, *pusillula* maintained nearly the same fluid consumption on 25% seawater as on tap water and increased its consumption slightly, but insignificantly, while on 50% and 60% seawater (Fig. 2, Table 3). On the other hand, mean consumption of 50% seawater by *gouldii* was nearly double that of tap water (Fig. 2, Table 3).

The fluid consumption responses of tolerant and nontolerant birds of both races on stressful drinking solutions (50 to 70% seawater) were examined independently of the above results. Typical responses of tolerant *pusillula* on these regimens show that these birds tended to increase their consumption only slightly above the level seen on the previous regimen (Table 4). Tolerant *gouldii* on 50% seawater (none were tolerant above 50% seawater) increased their consumption to much higher levels than *pusillula*. The responses seen in nontolerant birds of both races were highly varied such that definite trends were not apparent.

Both *pusillula* and *gouldii* maintained body weight effectively on tap water and 25% seawater (Fig. 3). On 50% seawater *pusillula* maintained body weight more effectively than *gouldii* (Fig. 3). However, due to the small sample size and high variance in *gouldii* this difference is not statistically significant. Most birds of both subspe-

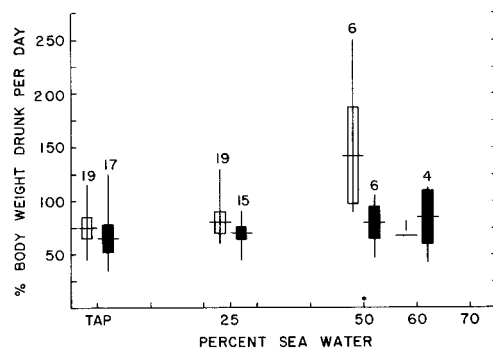


FIGURE 2. The relationship between fluid consumption and percent seawater in drinking solutions. Includes only birds (*n* above each symbol) successfully maintained for 4 or more days on each dilution. Open boxes indicate ± 2 SE of mean for *gouldii* and black boxes ± 2 SE of mean for *pusillula*. The horizontal line represents the range. An asterisk above percent of seawater indicates significant difference between means (*t*-test, *P* < 0.05).

cies failed on this regimen. Graduation of the birds from 25% seawater (approximately 270 mOsmols/l) to 50% seawater (approximately 540 mOsmols/l) undoubtedly represents the transition from a hypoosmotic to a hyperosmotic drinking solution. While plasma osmolarities were not measured for *pusillula* or *gouldii* it seems

TABLE 3. Fluid intake and weight change in *M. m. pusillula* and *M. m. gouldii* on increasing salinities of drinking solution.^a

Drinking solution	<i>M. m. pusillula</i>				<i>M. m. gouldii</i>			
	<i>n</i>	Mean initial wt. (g)	% wt. change/day	Intake as % body wt./day	<i>n</i>	Mean initial wt. (g)	% wt. change/day	Intake as % body wt./day
Percentages of seawater								
0	22	17.9	-0.3 \pm 0.1	65 \pm 14	22	18.7	-0.1 \pm 0.1	75 \pm 9
25	20	18.0	+0.1 \pm 0.1	70 \pm 6	22	18.8	+0.1 \pm 0.1	81 \pm 9
50	6	18.2	-0.2 \pm 0.1	79 \pm 16	7	17.8	-1.5 \pm 1.6	142 \pm 45
60	4	17.2	-1.9 \pm 2.6	84 \pm 26	1	16.8	-1.9 —	67 —
Molarity NaCl								
0.00	15	18.0	+0.1 \pm 0.1	76 \pm 10	17	18.8	+0.1 \pm 0.1	85 \pm 15
0.11	18	18.3	+0.2 \pm 0.1	80 \pm 2	18	19.3	+0.2 \pm 0.4	95 \pm 13
0.16	18	18.4	+0.1 \pm 0.1	77 \pm 12	17	19.7	+0.1 \pm 0.1	102 \pm 12
0.22	18	18.4	+0.1 \pm 0.1	79 \pm 10	19	19.4	-0.3 \pm 0.1	139 \pm 26
0.27	18	18.3	+0.1 \pm 0.1	79 \pm 5	17	18.3	-0.7 \pm 0.2	190 \pm 6
0.32	16	17.0	-0.5 \pm 0.3	89 \pm 13	10	16.7	-1.8 \pm 0.1	124 \pm 24
0.38	9	17.6	-0.9 \pm 1.1	96 \pm 12	0	—	—	—
0.43	3	16.2	-2.9 \pm 0.5	137 \pm 70	0	—	—	—

^a Does not include data from birds which appeared to waste water by shaking their heads while drinking. Includes tolerant birds (listed in Table 2) as well as nontolerant birds which appeared tolerant for 4 or more days prior to failure.

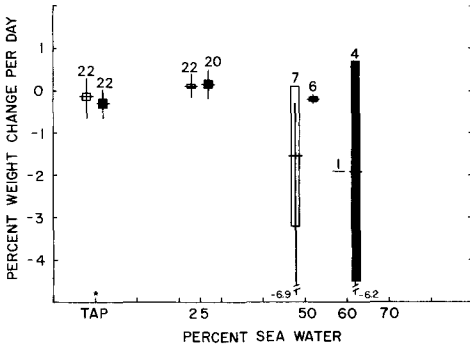


FIGURE 3. The relationship between maintenance of body weight and percent seawater in drinking solution. Includes only birds (n above each symbol) successfully maintained for 4 or more days on each dilution. Open boxes indicate ±2 SE of mean for *gouldii* and black boxes ±2 SE of mean for *pusillula*. The horizontal line is the mean and the vertical line represents the range. An asterisk above percent of seawater indicates significant difference between means (t-test, P < 0.05).

reasonable to assume that they fall within the 310 to 370 mOsmols/l range seen in other fringillids such as Sage Sparrows, *Amphispiza belli nevadensis* (Moldenhauer and Wiens 1970), House Finches, *Carpodacus mexicanus* (Poulson and Bartholomew 1962a) and Savannah Sparrows, *P. s. brooksi* (Poulson and Bartholomew 1962b). No *gouldii* and only two *pusillula* tolerated the 60% seawater regimen (Table 2).

A possible dichotomy in the ability to maintain body weight is seen on the 50% seawater regimen (Fig. 4). Tolerant *pusillula* were able to maintain body weight more closely to the mean initial value than were tolerant *gouldii*. This is also shown in Figure 3 where the percent daily weight change is less in *pusillula* than in *gouldii*.

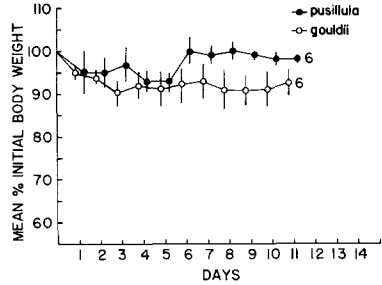


FIGURE 4. Typical patterns of the relationship between percent of initial body weight and time (in days) for birds drinking solutions of 50% seawater. Includes only birds tolerant for the entire regimen. The vertical line represents ±2 SE of mean for *gouldii* (open circles) and *pusillula* (closed circles).

Perhaps tolerant *pusillula* were better able to process and adjust to hyperosmotic seawater solutions. There appeared to be little difference in the abilities of nontolerant *pusillula* and *gouldii* to maintain body weight on stressful seawater solutions.

The two types of seawater drinking responses seen in *pusillula* and *gouldii* can to some extent be correlated with the changes in body weight. As *gouldii* increased its consumption slightly, but not significantly, on 25% seawater (Fig. 2), a slight increase in body weight was observed (Fig. 3). Thus, *gouldii* were effectively able to process this solution. However, as *gouldii* increased its consumption significantly on 50% seawater (Fig. 2) a corresponding decline in body weight was observed (Fig. 3). On hypertonic drinking solutions the normal osmotic gradient between the gut and bloodstream is reversed resulting in a net loss of body fluids to the gut. In contrast, *pusillula* increased its fluid consumption only slightly between tap water and 60% seawater (Fig. 2), while

TABLE 4. Weight change and fluid intake in *M. m. pusillula* and *M. m. gouldii* which tolerated stressful hyperosmotic drinking solutions.*

Drinking solution	<i>M. m. pusillula</i>				<i>M. m. gouldii</i>			
	n	Mean initial wt. (g)	Intake as % body wt./day	Mean end wt. as % initial wt.	n	Mean initial wt. (g)	Intake as % body wt./day	Mean end wt. as % initial wt.
Percentages of seawater								
50	6	18.5	78	98	6	18.6	142	92
60	2	17.0	101	101	0	—	—	—
Molarity NaCl								
0.32	15	18.3	90	98	5	17.9	134	96
0.38	7	17.6	98	100	0	—	—	—

* These data include only tolerant birds. Hence, they differ from those in other tables which include nontolerant birds as well.

exhibiting a correspondingly nonsignificant decrease in body weight (Fig. 3).

RESPONSES TO NaCl DRINKING SOLUTIONS

Results obtained from the NaCl regimens appear to be more instructive. For this series of tests the concentration of the drinking solution was increased more gradually, thus allowing the birds more time to acclimate to each solution. On these regimens the graduation from hypoosmotic to hyperosmotic drinking solution most probably occurred between 0.16 M NaCl (approximately 324 mOsmols/l) and 0.22 M NaCl (approximately 432 mOsmols/l). On NaCl molarities of 0.00 M (distilled water), 0.11 M, 0.16 M, 0.22 M, and 0.27 M NaCl *pusillula* and *gouldii* were essentially equally tolerant (Table 2). Beyond 0.27 M NaCl a dichotomy in tolerance between races is clearly seen. Fifteen of 18 *pusillula* (83%) were maintained successfully for 13 days on 0.32 M NaCl compared to only six of 17 *gouldii* (35%). None of these six *gouldii* was able to accommodate to 0.38 M NaCl, while seven of the 15 *pusillula* made the accommodation (Table 2). Of these seven *pusillula* six failed to maintain themselves beyond 4 days on 0.43 M NaCl. The seventh bird was maintained for 10 days prior to failing the regimen.

The results on fluid consumption obtained for the NaCl regimens were very similar to those obtained for the seawater regimens. As the concentration of the drinking solution was increased, *gouldii* increased its consumption slightly on 0.11 M and 0.16 M NaCl solutions. However, in the transition to hyperosmotic drinking solutions of 0.22 M and 0.27 M NaCl, *gouldii* increased its consumption dramatically (Fig. 5). At 0.32 M NaCl *gouldii* decreased its consumption. As was the case on the seawater regimens, *pusillula* held its consumption of NaCl solutions relatively constant from distilled water through 0.27 M NaCl. Even on hyperosmotic regimens of higher NaCl concentration (0.32 M, 0.38 M, and 0.43 M), *pusillula* increased its consumption slightly, but not significantly, over each previous concentration (Fig. 5). Significant differences (*t*-test, $P < 0.05$) in the fluid consumption patterns of *pusillula* and *gouldii* were seen at 0.16 M, 0.22 M, 0.27 M, and 0.32 M NaCl (Fig. 5).

Both races maintained weight effectively on distilled water, 0.11 M and 0.16 M NaCl solutions (Fig. 6 and Table 3). On hyperosmotic solutions at 0.22 M and 0.27 M, *gouldii*, although

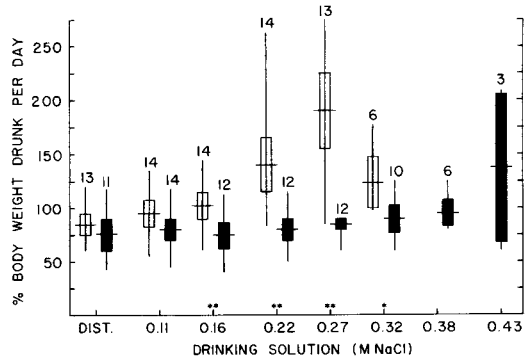


FIGURE 5. The relationship between fluid consumption and concentration of drinking solution (M NaCl). Includes only birds (n above each symbol) successfully maintained for 4 or more days on each dilution. Open boxes indicate ± 2 SE of mean for *gouldii* and black boxes ± 2 SE of mean for *pusillula*. The horizontal line represents the range. An asterisk above molarity indicates significant difference between means (*t*-test, $P < 0.05$) and 2 asterisks ($P < 0.01$).

still tolerant, tended to lose body weight while *pusillula* maintained body weight quite effectively. Significant (*t*-test, $P < 0.05$) weight loss was noted in both subspecies on 0.32 M NaCl (Fig. 6). If all individuals are considered, *gouldii* lost more weight (2% per day) than *pusillula* (1% per day) (Table 3). If only tolerant individuals are examined, *pusillula* typically maintained its weight very close to initial levels (97 to 99%) compared to *gouldii* (94 to 97%) (Table 4). Our observations of the tested birds suggest that *pusillula* was more tolerant of weight loss. Individuals remained alert and active at levels as low as 70 to 80% of initial body weight compared to equivalent responses at 80 to 90% of initial body weight in *gouldii*. This suggests that *gouldii* not tolerant of hyperosmotic regimens were either already stressed when the regimen began or they were somewhat less tolerant of weight loss than *pusillula*. The fact that mean initial body weight for *gouldii* was slightly lower than *pusillula*'s suggests that the *gouldii* were already stressed, for *gouldii* tend to be somewhat heavier than *pusillula* under natural conditions (Table 3). It is further interesting to note that the mean upper limit of daily weight loss for all tests was -1.80% for *gouldii* (0.32 M NaCl) compared to -2.95% for *pusillula* (0.43 M NaCl). Thus *pusillula* may in fact be more tolerant of weight loss. This is an adaptation that could be quite useful during

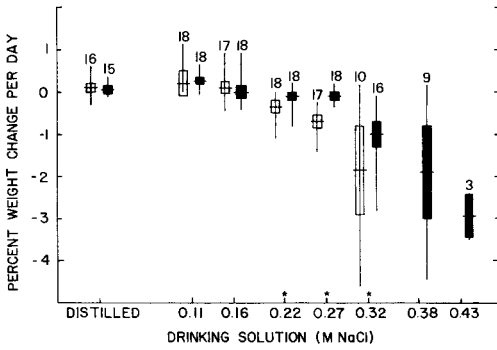


FIGURE 6. The relationship between maintenance of body weight and concentration of drinking solution (M NaCl). Includes only birds (n above each symbol) successfully maintained for 4 or more days on each dilution. Open boxes indicate ± 2 SE of mean for *gouldii* and black boxes ± 2 SE of mean for *pusillula*. The horizontal line is the mean and the vertical line represents the range. An asterisk above percent of seawater indicates significant difference between means (t -test, $P < 0.05$).

periods when suitable water is scarce in their natural habitat.

As in the case of the seawater regimens, it is possible to correlate fluid consumption with weight change in both *pusillula* and *gouldii* on NaCl solutions. *Gouldii* increased its fluid consumption gradually between distilled water and 0.16 M NaCl (Fig. 5). On these regimens little weight loss was noticed (Fig. 6). On 0.22 M and 0.27 M NaCl, which were presumably hyperosmotic, *gouldii* increased its consumption sharply (Fig. 5) and a corresponding weight loss was seen (Fig. 6). On 0.32 M NaCl *gouldii* decreased its consumption (Fig. 5) but weight loss still resulted (Fig. 6). It seems logical to assume, therefore, that it became increasingly more difficult for

gouldii to extract physiologically useful water from NaCl solutions more concentrated than 0.16 M. The slight increase in water consumption shown by *pusillula* on NaCl solutions was not nearly as pronounced as that seen by *gouldii* (Fig. 5). Likewise the body weight of *pusillula* was more nearly stable (Fig. 6). Both body weight and fluid consumption for *pusillula* remained relatively constant through 0.27 M NaCl (Figs. 5, 6). On 0.32 M, 0.38 M, and 0.43 M NaCl *pusillula* showed gradual, but not significant, increases in fluid consumption (Fig. 5). However, there was a sharp, statistically significant (Student's t -test, $P < 0.01$) decrease in body weight (Fig. 6).

SALT INTAKE

Table 5 shows the average daily salt intake as percent body weight for *pusillula* and *gouldii* on all regimens except tap and distilled water. From these results and those on freshwater consumption it is clear that neither race was able to regulate its intake of NaCl. *Pusillula* does regulate its overall fluid consumption at NaCl concentrations below 0.32 M (Table 3, Figs. 2, 5). The increase in its consumption beyond 0.32 M is not nearly as rapid as that seen in *gouldii* at much lower concentrations (Table 3). It appears, therefore, that *pusillula* is better able to tolerate a higher level of NaCl intake.

DISCUSSION

The responses of both *pusillula* and *gouldii* on the initial seawater regimens are typical of at least some other salt-marsh and upland species. Bartholomew and Cade (1963) have classified and thoroughly explained the drinking patterns of land-

TABLE 5. Mean salt intake per day as percent of initial body weight for *M. m. pusillula* and *M. m. gouldii*.

	% seawater			Molarity NaCl						
	25	50	60	0.11	0.16	0.22	0.27	0.32	0.38	0.43
<i>M. m. pusillula</i>										
Mean salt intake as % body wt.	0.55	1.25	1.57	0.51	0.72	1.02	1.25	1.66	2.14	3.44
± 2 SE	0.05	0.26	0.48	0.08	0.11	0.13	0.08	0.24	0.28	1.76
No. birds	15	6	4	14	12	12	12	10	6	3
<i>M. m. gouldii</i>										
Mean salt intake as % body wt.	0.64	2.24	1.27	0.61	0.96	1.78	2.99	2.31	—	—
± 2 SE	0.07	0.70	—	0.08	0.11	0.33	0.54	0.44	—	—
No. birds	19	6	1	14	14	14	13	6	—	—

birds into three general categories summarized here:

PATTERN A

Birds in this category greatly increase the amount of fluid consumed as the salinity of the drinking solution is increased until some critical concentration is reached at which time fluid consumption is greatly decreased. Individuals may even refuse to drink altogether even though heavy weight loss may have already occurred. The House Finch, three freshwater marsh races of the Savannah Sparrow, *P. s. brooksi*, *P. s. nevadensis*, and *P. s. anthinus* as well as *M. m. cooperi* (freshwater marsh race) all exhibit this type of response (Bartholomew and Cade 1963). The Gambel White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) also greatly increases its fluid consumption in response to increasing drinking fluid salinity (MacMillen and Snelling 1966).

PATTERN B

Birds in this category tend to drink virtually the same amount of fluid exclusive of the salinity of the drinking solution. The California Quail (*Callipepla californica*) tends to fit this pattern (Bartholomew and Cade 1963).

PATTERN C

This pattern is typically exhibited by Savannah and Song sparrows inhabiting salt marshes, *P. s. beldingi* and *P. s. rostratus* as well as *M. m. maxillaris* and *M. m. samuelis*. These birds tend to have a very high ad libitum consumption of distilled water with respect to body mass. As the salinity of the drinking solution is increased, water consumption either decreases or remains relatively constant (Bartholomew and Cade 1963).

On the seawater regimes *pusillula* showed a drinking response that is somewhat typical of other salt-marsh fringillids. Its fluid consumption remained relatively constant, compared to that of *gouldii* (which increased markedly) with increasing salinity of the drinking solution. No sharp increase in fluid consumption was seen in the transition from hypoosmotic to hyperosmotic drinking solutions. It should be pointed out, however, that *pusillula's* ad libitum fluid intake did increase slightly each time the concentration of the drinking solution was increased. Fluid consumption for *pusillula* on tap water was 69.6% of body weight while consumption of 60%

seawater was found to be 84.0% of body weight (Table 3). This response is in contrast to that seen in salt-marsh Savannah Sparrows (*P. s. beldingi* and *P. s. rostratus*) which tended to decrease consumption as the salinity of the drinking solution was increased (Cade and Bartholomew 1959). Like other upland species *gouldii* greatly increased its fluid consumption as the salinity of the drinking solution increased. The only exception to this was seen on 60% seawater where *gouldii* decreased its consumption. This also is in accordance with the results seen with other upland species (Cade and Bartholomew 1959, Bartholomew and Cade 1963). As *gouldii* increased its consumption on hyperosmotic seawater solutions, most individuals showed a corresponding loss in body weight. In contrast, *pusillula* generally did not show precipitous losses in body weight unless fluid consumption was greatly curtailed. In any case, *pusillula* showed a greater ability to survive in spite of heavy weight loss. This held true regardless of the level of fluid consumption (Table 3). This strategy would be extremely useful during prolonged hot weather.

Whereas in *pusillula* fluid consumption increased moderately at each increase in salinity (Table 3, Figs. 2, 5), in salt-marsh Savannah Sparrows (*P. s. beldingi* and *P. s. rostratus*) fluid consumption dropped as salinity of the drinking solution increased (Cade and Bartholomew 1959). This increase in consumption is, however, very similar to that seen for the salt-marsh Seaside Sparrow, *Ammodramus maritimus maritimus*. This subspecies, which is perhaps an eastern ecological counterpart to *pusillula*, showed an increase in daily ad libitum fluid consumption from 52.0% of body weight on distilled water to 142.8% of body weight on 0.40 M NaCl (Poulson 1969).

Bartholomew and Cade (1963) described the drinking responses for several upland and salt-marsh species including *M. m. maxillaris* and *M. m. samuelis*. However, it is not clear from their description whether these birds decreased, held constant, or increased their level of fluid consumption with increasing salinity of the drinking solution. In any case the studies on *maxillaris* and *samuelis* were preliminary, were conducted using a small sample size (approximately six birds) of each race, and the original data are no longer available (Cade, pers. comm.). The pattern of increasing consumption slightly at higher salinities as seen in *pusillula* may in fact be typical of *maxillaris* and *samuelis* as well.

TABLE 6. Mean body weight and ad libitum fresh water consumption in several fringillid species.

Species	Mean body weight (g)	Mean ad libitum fluid consumption (% body wt./day)	Source
<i>Melospiza melodia pusillula</i>	17.9	65.1	Present study
<i>M. m. pusillula</i>	18.0	76.1	Present study
<i>M. m. gouldii</i>	18.7	75.5	Present study
<i>M. m. gouldii</i>	18.8	86.6	Present study
<i>M. m. maxillaris</i>	18.2	41.8	Bartholomew and Cade (1963)
<i>M. m. samuelis</i>	16.4	52.5	Bartholomew and Cade (1963)
<i>M. m. cooperi</i>	16.8	21.2	Bartholomew and Cade (1963)
<i>Passerculus sandwichensis brooksi</i>	17.5	58.2	Bartholomew and Cade (1963)
<i>P. s. beldingi</i>	17.0	100.0	Bartholomew and Cade (1963)
<i>P. s. rostratus</i>	19.0	69.0	Bartholomew and Cade (1963)
<i>Ammodramus maritimus maritimus</i>	19.0–24.0	52.0	Poulson (1969)
<i>A. caudacuta caudacuta</i>	13.0–17.0	75.0–88.0	Poulson (1969)
<i>A. c. subvirgata</i>	17.0–19.0	33.0	Poulson (1969)
<i>Zonotrichia leucophrys gambelii</i>	26.9–31.6	45.6	MacMillen and Snelling (1966)

Some mention should be made of the relative ad libitum distilled/tap water consumption of *pusillula* and *gouldii* compared to those other species. Table 6 shows ad libitum freshwater consumption in the absence of temperature stress for *pusillula* and *gouldii* as well as for other species. On both distilled water and tap water *gouldii* showed a higher but not significantly different level of fluid consumption than *pusillula*.

This higher consumption of fresh water by the upland race (*gouldii*) than the salt-marsh race (*pusillula*) contrasts with the pattern found by Bartholomew and Cade (1963) in Savannah Sparrows. They found the upland race, *P. s. brooksi*, to consume less fresh water than the two salt-marsh races, *P. s. beldingi* and *P. s. rostratus* (Table 6). Based on its relative salt tolerance and the patterns discussed by Bartholomew and Cade one would expect *gouldii* to show a lower value of freshwater consumption; this is clearly not the case. In fact to the best of our knowledge this represents the first instance where an upland population showed a higher level of ad libitum freshwater consumption than its salt-marsh counterpart.

Mean daily ad libitum freshwater consumption for *pusillula* (65 to 76% body weight per day) was found to correspond closely to the consumption found in other salt-marsh fringillids, *P. s. rostratus* (69.0%), *P. s. beldingi* (100%), and *A. c. caudacuta* (75 to 88%) (see Table 6). Interestingly, ad libitum consumption in our *pusillula* was higher than Cade and Bartholomew (1963) found in their preliminary tests on *M. m. max-*

illaris (41.8%) and *M. m. samuelis* (52.5%). It might be expected that all three races of San Francisco Bay salt-marsh Song Sparrows would have similar levels of ad libitum freshwater consumption. Further work should be done on the four races of San Francisco Bay area Song Sparrows.

HABITAT CONSIDERATIONS

To inhabit successfully the salt marshes of San Francisco Bay, sedentary birds such as *pusillula* must be able to tolerate water salinities ranging from 0.15 M to 0.37 M NaCl (Table 1). It is likely that salinities greater than 0.35 M NaCl are relatively rare and probably occur only on the warmest days and when the high tides are relatively low. Such periods of high salinity, coupled with lack of fog-drip or dew, seldom last more than 2 or 3 days. Because 15 of 18 of our *pusillula* maintained themselves for 13 days on 0.32 M NaCl, and thereafter seven of these 15 maintained themselves for a similar period on 0.38 M NaCl, they appear well adapted to survive saline stress for periods of several days in their natural habitat.

Interestingly, no account can be found of *pusillula*, *samuelis*, and *maxillaris* drinking the water in their natural environment. Our own field observations of *pusillula* failed to identify drinking behavior for any of the birds studied. It is worth noting that Tompa (1964) observed *M. m. morphna* drinking pure seawater on a few occasions on Mandarte Island, British Columbia, Canada. Salt-marsh Song Sparrows are known

to feed extensively on insects and various invertebrates that inhabit the salt-marsh mud (Johnston 1968). These undoubtedly account for a substantial source of preformed water when available. But during late summer and early fall, populations of insects decline and seeds become an important food source. This happens at a time when bay salinity is at its peak so that the ability to utilize bay water would be highly advantageous.

DISTRIBUTION

The distribution of *M. m. gouldii*, *M. m. pusillula*, *M. m. samuelis*, and *M. m. maxillaris* have been discussed by several authors (Grinnell 1913; Miller 1947, 1956; Marshall 1948a, 1948b; Johnston 1956a, 1956b; Ferrell 1966; Halliburton and Mewaldt 1976; Walton 1978). Each of the above studies list many of the same basic parameters which seem to control the distribution of these birds.

Gouldii, the upland subspecies, comes into limited contact with each of the other races at the mouths of the various drainages which empty into the bay system. *Maxillaris* resides in the marshes surrounding Suisun Bay which are definitely brackish (Marshall 1948a). *Samuelis* is present in the salt marshes of San Pablo Bay but these marshes are not as saline as those inhabited by *pusillula* on San Francisco Bay (Marshall 1948a). Thus, each of these races resides in a slightly different habitat. When Grinnell (1913) studied the birds of the now famous "willow patch" near Palo Alto, he hypothesized that both *pusillula* and *gouldii* showed a strong degree of habitat preference. Although these birds were residing in very close contact, interbreeding was found to be almost nonexistent.

The differing morphologies of the four races are discussed in detail by Marshall (1948a, 1948b). That each race exhibits distinct morphological characteristics indicates these birds are isolated from one another. Geographical isolation tends to enhance random fixation (genetic drift) which in turn leads to racial differentiation (Miller 1947). Marshall (1948a, 1948b) was able to correlate the degree of morphological differentiation of these birds with the degree to which they were isolated geographically. He also described clines in various morphological characters (bill depth, wing length, coloration, etc.) that exist between populations. With only one exception none of these clines followed any observable

environmental gradient. Interestingly, Marshall (1948a, 1948b) was able to show that yellow ventral coloration in salt-marsh subspecies followed the salinity gradient of the bay system. *Pusillula* shows the most yellow coloration and inhabits the marshes of San Francisco Bay which are most saline. Marshall (1948a, 1948b) attributed the high degree of observed racial and clinal differentiation to two factors: (1) spatial isolation between both subspecies and populations which leads to decreased gene flow and (2) differential but undefined selective pressures.

Several studies have found various resident Song Sparrow populations to be highly sedentary. Adults tend to remain faithful to the same territories in successive years (Nice 1937; Miller 1947, 1956). Dispersal distances for fledglings are extremely low. Mean dispersal distance for juveniles was found to be 225 m for *gouldii* (Halliburton and Mewaldt 1976) and 185 m for *samuelis* (Johnston 1956a, 1956b). Both of these factors tend to enhance random genetic fixation or genetic drift (Miller 1947).

While dispersal data have only been collected for *samuelis* and *gouldii* there is little reason to believe that *maxillaris* and *pusillula* behave differently. The overwhelming evidence thus far suggests that resident Song Sparrow populations are extremely sedentary. Size of an effective breeding population of Song Sparrows in Ohio (Nice 1937) has been estimated at 150 adults by Miller (1947). Allowing that such small populations are effective units, genetic drift could easily account for the morphological differences (e.g., clines) seen between populations as well as between races of the San Francisco Bay area Song Sparrows.

In addition to those morphological differences studied by Marshall (1948a, 1948b), Ferrell (1966) found significant differences in blood group frequencies between the races. Interestingly, he found some differences between populations were even more significant than between the races. Apparently the amount of racial variation seen is in some way "inundated" by variations at the population level. Ferrell, unable to explain fully these results, suggested that unknown selective pressures might play a key role. Halliburton and Mewaldt (1976) also emphasized the important role that natural selection might play in the results obtained by Ferrell. They noted that the few juveniles of each generation who tend to disperse well beyond the effective breeding unit may

be enough to offset the effects of random genetic drift between populations. This would tend to keep the populations within each of the four races of San Francisco Bay area Song Sparrows more nearly alike. Since there are racial differences, natural selection must play a role in the formation and maintenance of those differences.

There has been little discussion of the role that natural selection must have played in determining the morphologies and distribution of San Francisco Bay Song Sparrows. This is probably because no selective agent has yet been identified. It seems plausible to suggest that salt-marsh salinity, as a selective agent, may have played a role in determining and maintaining the distribution of *pusillula* and *gouldii* in the southern reaches of San Francisco Bay. *Pusillula* has adaptations that enable it to utilize hyperosmotic solutions, at least as saline as those found in San Francisco Bay while *gouldii* does not. This then would suggest that *gouldii* is simply not capable of surviving in the salt marshes of this region. Any individual *gouldii* dispersing into this region would tend to be selected against. Selective agents which might prevent *pusillula* from successfully entering a freshwater riparian habitat have not been identified in this study, however, body size and weight may play a key role. Mean body weight in *gouldii* is approximately 7% greater than that of *pusillula* (Marshall 1948b). Equipped with greater body mass, territorial *gouldii* males might well exclude *pusillula* from freshwater riparian habitat.

Since morphological differences exist between populations it is highly probable that physiological differences are also present. It is possible that different populations of *gouldii* inhabiting different regions around the bay may have differing salt tolerances. This possibility also exists between populations of *pusillula*, *samuelis*, and *maxillaris*. According to Aldrich (1984), as a species, *M. melodia* possesses sufficient genotypic plasticity to classify it as "one of the most ecogeographically variable birds in North America." While it does appear from the work done so far that *pusillula* has the greatest salt tolerance of the Song Sparrows inhabiting the San Francisco Bay region, the respective salt tolerances of the remaining two salt-marsh subspecies are unclear. A thorough understanding of the salt tolerances of these four subspecies could lend much towards understanding their respective distributions.

The activities of man have greatly affected

population size and distribution of salt-marsh Song Sparrows. During the period since 1850 the marshes surrounding the greater San Francisco Bay system have been reduced by approximately 75% mainly due to dredging, diking, and landfill projects (Walton 1978). Walton points out that habitat alteration and fragmentation have resulted in the formation of greater numbers of small breeding populations. Genetic drift among these small and widely scattered populations seems possible. Additionally, alteration of salt-marsh salinity may permanently alter the current distribution of salt-marsh populations.

The several Water Pollution (Sewage) Control Plants around San Francisco Bay are injecting hundreds of millions of gallons of fresh water into sloughs adjacent to some of the remaining salt marshes. One of these, Triangle Marsh, is adjacent to Coyote Creek which receives (via Artesian Slough) the effluent from the San Jose-Santa Clara Water Pollution Control Plant, now more than 100 million gallons of essentially fresh water daily. One of us (Mewaldt) has observed a gradual change in the plants which dominate Triangle Marsh over the last 30 years. Whereas in the 1950s it was dominated by pickleweed (*Salicornia pacifica*) and cord grass (*Spartina foliosa*), both typical salt-marsh dominants, now in the 1980s it is being taken over by alkali bulrush (*Scirpus robustus*), characteristic of brackish waters. The Song Sparrows here are typical *pusillula*. Upstream the sewage effluent flow in Artesian Slough, alkali bulrush gives way to California bulrush (*Scirpus californicus*) and finally cattails (*Typha latifolia* and *T. angustifolia*), typical of freshwater marshes. Thus in the otherwise more saline South San Francisco Bay, some marshes are becoming less saline. Bird banders from Coyote Creek Riparian Station report that many Artesian Slough captured Song Sparrows have the yellowish wash of *pusillula*. However, Song Sparrows captured in riparian habitat on nearby lower Coyote Creek seldom include birds with the yellowish wash and more resemble the upland *gouldii*. It will be interesting to see if *pusillula* and *gouldii* will maintain their identities in the man-altered habitats at the south end of San Francisco Bay. Decreased habitat salinity (and larger body size) may enable *gouldii* to exclude *pusillula* from some of its present range.

ACKNOWLEDGMENTS

We thank personnel of the San Francisco Bay National Wildlife Refuge for cooperation in providing access to

critical study areas. We thank Peggy J. Woodin, Jean Geary, and Diana Stillens for laboratory assistance, and Penny Delevoryas and Jim Shiomoto for field assistance. We are grateful to Deborah Basham for manuscript typing, Howard Shellhammer and Kenneth E. Hutton provided counsel and valuable insight in the planning of the study which yielded the M.S. thesis of the senior author at San Jose State University. Richard Warner and Robert Johnson provided computer assistance. We are grateful to Rob Klinger, Steven A. Laymon, and an anonymous reviewer for statistical advice, but we assume full responsibility for the methods we used. Richard E. MacMillen provided many useful ideas in his review of the manuscript.

LITERATURE CITED

- ALDRICH, J. W. 1984. Ecogeographical variation in size and proportions of Song Sparrows (*Melospiza melodia*). Ornithol. Monogr. No. 35, American Ornithologists' Union, Washington, DC.
- AMERICAN PUBLIC HEALTH ASSOCIATION (A.P.H.A.). 1976. Standard methods for the examination of water and wastewater. 14th ed. Washington, DC, p. 302-304.
- BARTHOLOMEW, G. A., AND T. J. CADE. 1963. The water economy of land birds. Auk 80:504-539.
- BASHAM, M. P. 1983. Salt tolerance in South San Francisco Bay Song Sparrows. M.Sc.thesis, San Jose State Univ., San Jose, CA.
- CADE, T. J., AND G. A. BARTHOLOMEW. 1959. Sea water utilization by Savannah Sparrows. Physiol. Zool. 32:230-238.
- FERRELL, G. T. 1966. Variation in blood group frequencies of Song Sparrows of the San Francisco Bay region. Evolution 20:369-382.
- GRINNELL, J. 1913. Notes on the palustrine faunas of west-central California. Univ. of Calif. Publ. Zool. 10:191-194.
- HALLIBURTON, R., AND L. R. MEWALT. 1976. Survival and mobility in a population of Pacific Coast Song Sparrows (*Melospiza melodia gouldii*). Condor 78:499-504.
- JOHNSTON, R. F. 1956a. Population structure in salt marsh Song Sparrows. Part I: Environment and annual cycle. Condor 58:24-44.
- JOHNSTON, R. F. 1956b. Population structure in salt marsh Song Sparrows. Part II: Density, age structure and maintenance. Condor 58:254-272.
- JOHNSTON, R. F. 1968. *Melospiza melodia*, p. 1547-1553. In O. L. Austin, Jr. [ed.], Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. Part 3. U.S. Natl. Mus. Bull. 237.
- MACMILLEN, R. E., AND J. C. SNELLING. 1966. Water economy of the White-crowned Sparrow and its use of saline water. Condor 68:388-395.
- MARSHALL, J. T. 1948a. Ecologic races of Song Sparrows in the San Francisco Bay region. Part I: Habitat and abundance. Condor 50:193-215.
- MARSHALL, J. T. 1948b. Ecologic races of Song Sparrows in the San Francisco Bay region. Part II: Geographic variation. Condor 50:233-256.
- MILLER, A. H. 1947. Panmixia and population size with reference to birds. Evolution 1:186-190.
- MILLER, A. H. 1956. Ecological factors which accelerate formation of races and species of territorial vertebrates. Evolution 10:262-277.
- MOLDENHAUER, R. R., AND J. A. WIENS. 1970. The water economy of the Sage Sparrow (*Amphispiza belli nevadensis*). Condor 72:265-275.
- NICE, M. M. 1937. Studies in the life history of the Song Sparrow, part I. A population study of the Song Sparrow and other passerines. Reprint, Dover Publications, Inc., New York.
- PEAKER, M., AND J. L. LINZILL. 1975. Salt glands in birds and reptiles. Cambridge Univ. Press, Cambridge.
- POULSON, T. L. 1969. Salt and water balance in Seaside and Sharp-tailed sparrows. Auk 86:473-489.
- POULSON, T. L., AND G. A. BARTHOLOMEW. 1962a. Salt utilization in the House Finch. Condor 64:245-252.
- POULSON, T. L., AND G. A. BARTHOLOMEW. 1962b. Salt balance in the Savannah Sparrow. Physiol. Zool. 35:109-119.
- TOMPA, F. S. 1964. Factors determining the numbers of Song Sparrows (*Melospiza melodia*) on Mandarte Island, B.C., Canada. Acta Zool. Fenn. 109.
- WALTON, B. J. 1978. The status of the salt marsh Song Sparrows of the San Francisco Bay system, 1974-1976. M.Sc.thesis, San Jose State Univ., San Jose, CA.