SALT WATER TOLERANCE AND WATER TURNOVER IN THE SNOWY PLOVER

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ABSTRACT.—A series of water-related experiments showed that Snowy Plovers do not have any outstanding physiological capabilities for dealing with the potential thermal and osmotic stresses of the Great Salt Plains, Oklahoma. Snowy Plovers and Semipalmated Sandpipers failed to maintain body weight when given 0.3 M NaCl *ad libitum*. Killdeer did even more poorly by rapidly losing weight on 0.2 M. These salt water tolerance values are limited when compared to other, particularly marine, birds that can drink full strength sea water. The Snowy Plover is no better at conserving water than other birds in its weight class. So plovers without drinking water were able to maintain their weight when furnished mealworm larvae *ad libitum*, the insectivorous diet as well as maintenance behavior of the birds is essential for their survival on the salt flats. *Department of Zoology, University of Oklahoma, Norman, Oklahoma 73069. Present address of first author: Quaternary Studies Center, Illinois State Museum, Springfield, Illinois 62706.* Accepted 3 October 1975.

THE Snowy Plover (*Charadrius alexandrinus*) is a small shorebird (30–40 g) common in habitats of high salinity (Bent 1929, Rittinghaus 1961). One such place is the Great Salt Plains in northwestern Oklahoma, a large, barren, salt-encrusted flat where the plover lives and breeds in abundance. The standing water on the salt plains, ranging in chloride concentration from 825.0 to 5156.0 mEq/l, is osmotically stressful to most organisms, yet the Snowy Plover centers its activities around many of these pools and watercourses (Purdue 1976a). The purpose of this study was to determine the physiological capability of the plover for utilizing hyperosmotic salt water. The plover's natural history and thermal ecology on the Great Salt Plains are treated elsewhere (Purdue 1976a, 1976b).

For comparison certain tests were also conducted on two other shorebirds, the Killdeer (*Charadrius vociferus*) and the Semipalmated Sandpiper (*Calidris pusillus*). The Killdeer breeds in normally vegetated habitats around the salt plains, but is seldom encountered on the salt flats, while the Sandpiper only migrates through the region on its way to breeding grounds in the north. Individual sandpipers often spend several days or more foraging around the saline waters on the salt flats.

METHODS

Birds were mist-netted or trapped on the salt flats and taken to laboratories at the University of Oklahoma in Norman, where they were acclimated to experimental conditions for at least 2 weeks, fed ground Purina Cat Chow (protein 30%, fat 8%, water 9.5–12%), and provided tap water *ad libitum*.

We conducted five experiments to determine tolerance to NaCl solutions: three on Snowy Plovers, and one each on Killdeer and Semipalmated Sandpipers. The concentration of NaCl in drinking water was gradually increased by 0.05 or 0.1 M increments until the birds were unable to maintain body weight. The length of time on each concentration varied from 3 to 11 days depending on the condition of the birds. The lengths of the regression lines (Fig. 1–3) with respect to the abscissa indicate the duration of treatment for each concentration. The plover species were allowed two days of tap water between incremented increases in NaCl concentration. Inverted bottles or graduated cylinders introduced water into small drinking cups. When salt water was given to the birds, they were taught to use rodent watering tubes in order to avoid an upward shift in salt concentration by evaporation from the drinking cups. Environmental conditions in the test chambers varied slightly between experiments because of the need to cooperate with other investigators. Two of the Snowy Plover and the Killdeer experiments were conducted at 33°C, relative humidity (RH) = 28 to 44%, and a photoperiod of 13 h light and 11 h dark (L:D = 13:11). The other Snowy

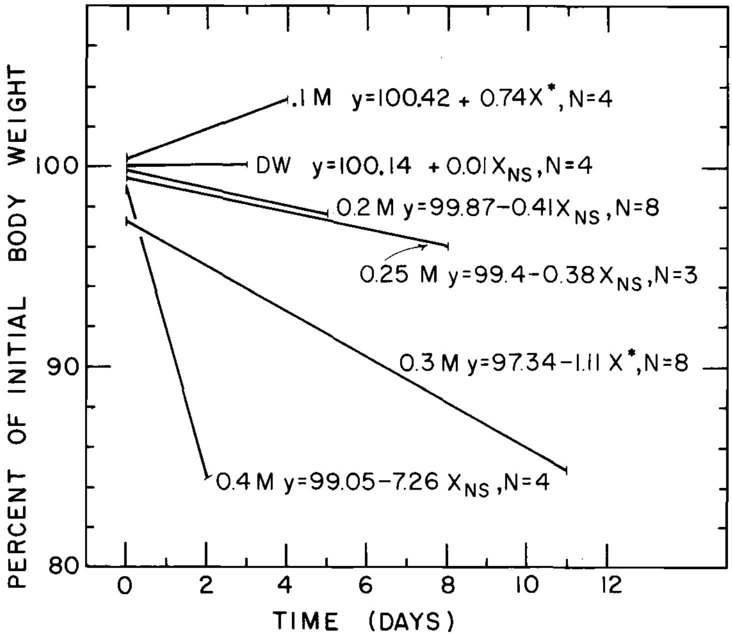

Fig. 1. Effect of salt water *ad libitum* on body weight of Snowy Plovers. N = sample size at beginning of Test, * = significant regression coefficient ($P < 0.05$), NS = nonsignificant regression coefficient.

Plover test—when the NaCl solution was 0.25 M—and the Semipalmated Sandpiper experiment took place at 25°C, RH = 30%, and L:D = 11:13.

Water deprivation tests on Snowy Plovers were conducted at 33°C, RH = 28 to 44%, and L:D = 13:11. Mealworms were fed *ad libitum* to a series of plovers deprived of any free water and body weight was monitored daily.

Tritiated water turnover was measured on Snowy Plovers, Killdeer, and Semipalmated Sandpipers at 25°C (L:D = 11:13, RH = 30%) and 40°C (L:D = 11:13, RH = 13%). The birds, which were in a steady state as indicated by constancy of body weight, were injected intraperitoneally with 50 μl of 0.52 μCi/μl tritiated water (THO). At least two blood samples (10 to 25 μl plasma) were taken from the brachial vein within 4 h of injection and subsequently single samples were taken daily. Each sample was centrifuged; the plasma was transferred to a toluene/butyl PBD/PBDO scintillation solution and counted (Beckman LS-133). Half life (T ½) was determined from the slope of the linear regression between the log of relative concentration (C_t) of plasma THO and time in days. C_t is the ratio of cpm/ml at time (t) divided by cpm/ml observed at the initial blood sampling. The equation for determining the fraction of water exchanged daily (λ) is:

$$\lambda = \frac{0.693}{T\,½} .$$

Total water content was estimated from the following relationship:

$$V_{H_2O} = \frac{(cts_i)(v_i)}{cts_o}$$

where V_{H_2O} = total water content in ml, cts_i = cpm/ml injected, v_i = volume of THO injected in ml, cts_o = the zero time value of the equation $cts_t = cts_o e^{-\lambda t}$ in which cts_t is the plasma cpm/ ml at t, and t = time in days. Daily water turnover was determined by the following equation:

$$\dot{V}_{H_2O} = V_{H_2O} \cdot \lambda$$

where $\dot{V}_{H_2O}$ = daily water turnover in ml/day. Both V_{H_2O} and $\dot{V}_{H_2O}$ were relativized by dividing by body weight.

All statistical tests (significance of regression coefficients and analysis of variance) were done in accordance with Sokal and Rohlf (1969).

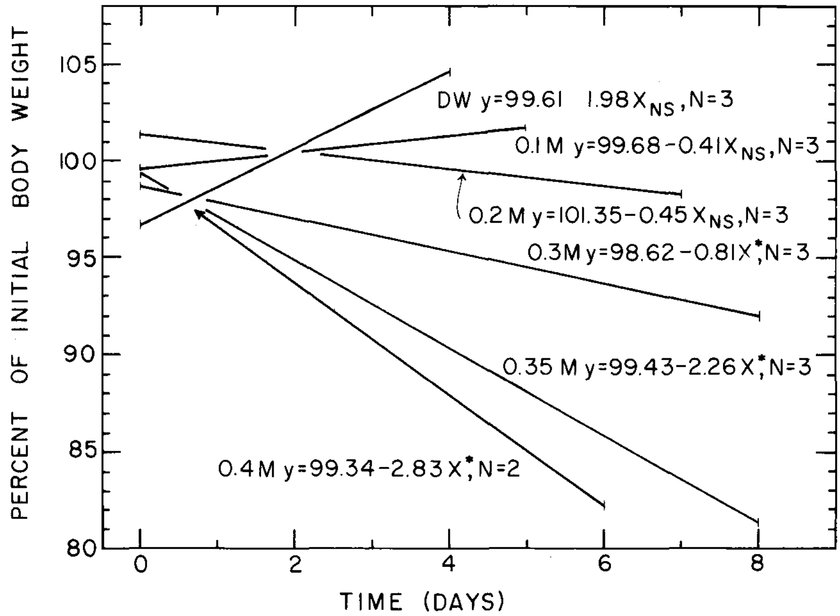

Fig. 2. Effect of salt water *ad libitum* on body weight of Semipalmated Sandpipers. Abbreviations given in Fig. 1.

RESULTS

Salt water tolerance.—The Snowy Plover (Fig. 1) and the Semipalmated Sandpiper (Fig. 2) were able to maintain or gain body weight at salinities of 0.2 to 0.25 M NaCl. At 0.3 M significant weight loss occurred in both species, but weight loss was slow and the birds survived for more than a week. Weight loss in the Snowy Plover (Fig. 1) was precipitous at 0.4 M and death would have resulted if the birds

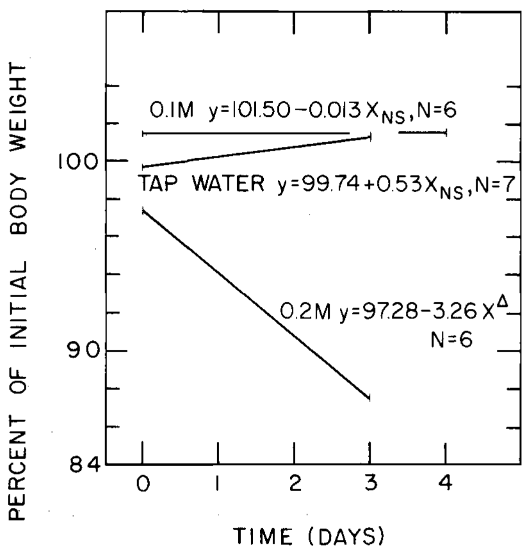

Fig. 3. Effect of salt water *ad libitum* on body weight of Killdeer. Abbreviations same as for Fig. 1 except △ = significant difference between days ($P < 0.05$), but nonsignificant regression coefficient.

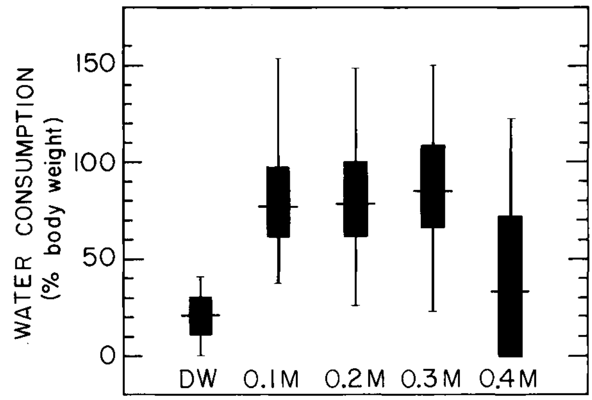

Fig. 4. Fluid consumption of Snowy Plovers at concentrations of NaCl. Ranges are indicated by length of vertical lines, means by horizontal lines, and 95% confidence limits either side of mean by darkened block. DW means distilled water.

had not been given fresh water. In the sandpiper (Fig. 2) weight loss at 0.35 M and 0.4 M was not as precipitous as in the Snowy Plover, but it was considerably more rapid than at 0.3 M. The sandpipers had no interruption in their salt water regime, but the plovers did, during the 2-day "tap water break" between molar increments. Thus the sandpipers may have been more fully acclimatized to salt water and lost weight at a slower rate.

The Killdeer (Fig. 3) did not maintain its weight at salinities above 0.1 M, and weight loss was precipitous at 0.2 M. Variability was great for the 0.2 M values, and the regression coefficient was not significant. There was, however, a significant decrease ($P < 0.05$) in percent of initial body weight between days. Overall, the sandpiper and the Snowy Plover were about equal in ability to tolerate salt water, with the sandpiper perhaps slightly better. The Killdeer was by far the least capable in this respect.

Water content.—Water constituted 69.6% and 72.8% of the body weight of Snowy Plovers in two separate tritiated water experiments (one at 25°C and one at 40°C) in which the birds were provided with tap water *ad libitum*. In a third test a group provided with 0.25 M NaCl was dehydrated to 62% (Table 1). The latter figure is significantly different ($P < 0.05$) from the other two according to the Student-

TABLE 1

MEAN WATER CONTENT AND DAILY WATER TURNOVER FOR SNOWY PLOVERS, SEMIPALMATED SANDPIPERS, AND KILLDEER.[1]

	N	Temp. (°C)	Mean Body Wt. (g)	Water Content (% body weight)	Daily Water Turnover (% body wt/day)
Snowy Plover (Tap water)	4	25	33.7	69.59 (± 1.85)	43.32 (± 1.05)
	4	40	32.2	72.75 (± 1.07)	48.45 (± 3.31)
Snowy Plover (0.25 M NaCl)	3	25	34.0	62.26 (± 2.56)	39.01 (± 1.73)
Semipalmated Sandpiper (Tap water)	3	25	24.3	58.50 (± 3.05)	54.45 (± 4.08)
	3	40	22.5	55.93 (± 2.42)	56.55 (± 7.29)
Killdeer (Tap water)	1	40	71.1	67.16	46.25

[1] Parenthetical numbers are standard errors. Drinking fluid was provided *ad libitum*.

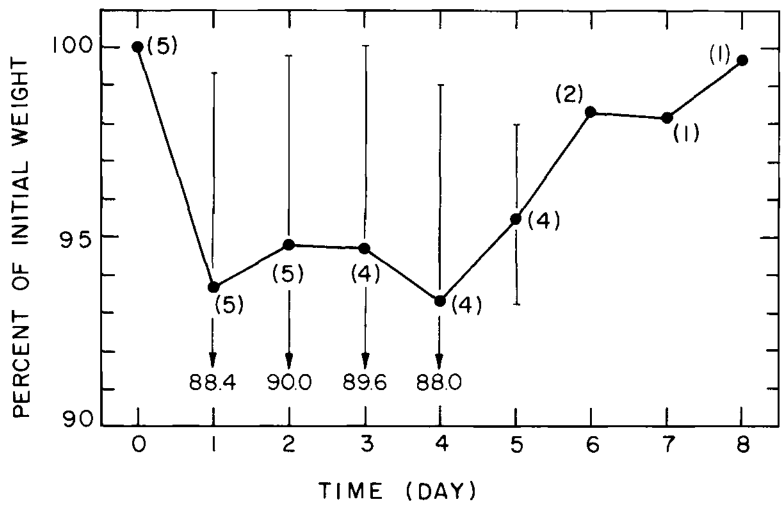

Fig. 5. Snowy Plovers maintained on mealworms *ad libitum* with no free water. Sample sizes in parentheses. Confidence limits (95%) around the mean are indicated by vertical lines.

Newman-Keuls *a posteriori* test that we used to isolate the deviant group indicated in a single-level analysis of variance (Sokal and Rohlf 1969). No difference was found between tap-watered birds kept at 25°C and those at 40°C. The plovers on 0.25 M NaCl were near the limit of their tolerance (Fig. 1) and showed a corresponding decrease in water content.

Semipalmated Sandpipers contained less water than Snowy Plovers held at comparable environmental conditions. A two-way analysis of variance for temperature and species indicated a significant difference between species ($P < 0.05$) but not between temperatures. These sandpipers were in migration when captured in the middle of May and as the experiment was conducted only 20 days later, they still may have had migratory fat or relatively heavier plumage that would have decreased the percentage of body water. In contrast, the Snowy Plovers that showed decreased water content (those drinking 0.25 M NaCl) had been in captivity for several months. One Semipalmated Sandpiper (not included in Table 1) that was held in captivity for several months had a water content of 67.6%, a figure in line with Snowy Plovers held at comparable conditons (40°C). A single Killdeer held at 40°C also was similar in water content (67.2%).

Fluid consumption and water turnover.—Fluid consumption was measured during the NaCl tolerance tests on Snowy Plovers (Fig. 4) and significant differences ($P < 0.05$) were found in drinking rates. Consumption was 20% of body weight per day when the birds were given distilled water. At moderate salinities, i.e. those that the plovers can tolerate for several days (Fig. 1), the increase in fluid intake was dramatic. At 0.4 M NaCl, the point of precipitous weight loss, fluid intake diminished sharply.

Although water turnover rates (Table 1) subjected to one- and two-way analysis of variance tests revealed no statistically significant differences between species or within given species under the different conditions, both the Snowy Plover and the Semipalmated Sandpiper bordered on significantly increased ($0.05 < P < 0.10$) turnover with increased ambient temperature: 43% at 25°C and 48% at 40°C for the plover and 54–57%, respectively, at comparable temperatures for the sandpiper. A slightly larger sample size probably would have confirmed this. A series of three Snowy Plovers on 0.25 M NaCl had slightly less turnover than plovers on tap water at the same temperature. A single Killdeer, held at 40°C, turned over 46% of its body weight each day.

Water deprivation.—Mealworm larvae were provided *ad libitum* as the only source of both food and water (Fig. 5) to a series of Snowy Plovers. After an initial drop in weight during the first day, the birds maintained or increased their weight. Unfortunately the test was hampered by a shortage of mealworms. As a result, it was necessary to remove some of the experimental birds. Nevertheless, the evidence is sufficient to show that the plovers could maintain body weight.

Discussion

The salt tolerance of the Snowy Plover, Killdeer, and Semipalmated Sandpiper does not appear to be exceptional when compared to other species of birds. Bartholomew and Cade (1963) listed the following species as being able to tolerate salinities in excess of 0.3 M: *Taeniopygia castanotis*, three subspecies of *Passerculus sandwichenesis*, and *Melospiza melodia cooperi*. Later MacMillen and Trost (1966) found that *Zenaida asiatica* and *Scardafella inca,* two common doves of the southwestern deserts of the United States, can withstand 37.5–50% sea water (equivalent to approximately 0.2 to 0.3 M NaCl). Three species of quail could not withstand more than 0.3 M NaCl (McNabb 1969). *Agelaius phoeneceus* tolerated up to 0.3 M NaCl (Hesse and Lustick 1972); *Amphispiza bilineata*, 0.4 M (Smyth and Bartholomew 1966); *Spizella breweri*, 0.55 M (Ohmart and Smith 1970); *Pooecetes gramineus*, 0.3 M (Ohmart and Smith 1971); and *Carpodacus mexicanus*, less than 0.3 M (Poulson and Bartholomew 1962). Frings and Frings (1959) found that two species of albatross could not survive in captivity unless artificial sea water was provided. Surprisingly little work has been reported on the salt tolerance of charadriiform birds even though their extrarenal salt glands are generally well developed and much studied. Hughes (1970) kept more than half of her sample of *Larus glaucescens* at constant weight when provided with 100% sea water (approximately 0.6 M NaCl) which is well beyond the limits tolerated by the three species we examined.

When provided NaCl solutions, encrustations appeared near the nasal openings of the plovers, indicating the presence of extrarenal salt glands. Staaland (1967) examined over 20 species of charadriiform birds for the size and function of nasal salt glands. He found that relative size of the gland was correlated with concentrating ability and ecology. Diversity of salt glands within the Charadriidae was evidenced by *Pluvialis apricaria* (body weight = 180 g) with a nasal gland (mg) to body weight (g) ratio of 0.3 while *Charadrius hiaticula* (49 g) had a ratio of 0.7. *Calidris canutus* (110 g) had the highest ratio (1.2) of Charadrii species. Our dissections showed that the salt gland of the Snowy Plover is slightly smaller than that shown for *Actitis hypoleucos* (47 g; diagramed in Staaland 1967), which had a ratio of 0.6. The Killdeer's salt gland is relatively smaller than the Snowy Plover's. This evidence supports the salt tolerance findings in that the Snowy Plover has a moderately developed salt gland and a correspondingly intermediate ability to handle high osmotic loads. The Killdeer with a relatively smaller gland displayed reduced salinity tolerance.

The Snowy Plover's level of fluid consumption at various salt concentrations (Fig.

4) is intermediate between Bartholomew and Cade's (1963) drinking patterns A and B. In pattern A, birds drink increasing amounts of water with increasing salinity until an upper limit is reached (0.4 M in this case) and consumption ceases. For pattern B, consumption is about the same across the entire range of salinities. According to Hesse and Lustick (1972) Red-winged Blackbirds (*Agelaius phoeniceus*) also had drinking characteristics that resembled both patterns A and B. Lustick (1970) suggested that the increase in drinking of tolerable salt water over distilled water may be the result of birds seeking salt.

As daily water turnover amounts to 43–48 (Table 1) of body weight and *ad libitum* distilled water consumption is 20% (Fig. 4), the remaining daily water requirement must consist of preformed and oxidative water from food and unlabeled water vapor in air across the lungs.

These experiments indicated that Snowy Plovers have similar water requirements to those of other avian species of similar body weight. Bartholomew and Cade (1963) compiled drinking water values for many bird species and showed a dramatic increase in relative water consumption for birds weighing 30 to 40 g or less. The Snowy Plover, which is in this weight class, fits in the pattern reported by Bartholomew and Cade.

Even though the Snowy Plover was not spectacular in its ability to tolerate salt or reduce water turnover, it does maintain body weight when fed mealworms, a substitute comparable to its natural food (Fig. 5). Its food, as discussed by Purdue (1976a), consists of flies, beetles, and other insects found on the salt plains. Insects, like other animals, have high water contents. Thus the insectivorous diet coupled with water-conserving behaviors, such as standing in pools during hot weather (Purdue 1976a), allows the Snowy Plover to avoid drinking the saline solutions that occur on the salt plains. Among other birds, Long-billed Marsh Wrens (*Telmatodytes palustris*) are also capable of survival on a diet of mealworms and no free water (Kale 1967); several passerine species and the Budgeriga (*Melopsittacus undulatus*) can maintain body weight when fed dry seeds (Bartholomew 1972); and two dove species from the North American deserts manage to live on succulent plants (MacMillen and Trost 1966).

Thus the Snowy Plover is another bird, such as the Horned Lark (*Eremophila alpestris*) (Trost 1972) and columbid species (MacMillen and Trost 1966), that has limited physiological capacities, yet lives in a seemingly osmotically-stressful environment. To survive in these habitats, the birds eat succulent foods and depend on appropriate maintenance behavior.

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