SALT TOLERANCE AND WATER REQUIREMENTS IN THE SALT-MARSH HARVEST MOUSE[1]

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INTRODUCTION

The salt-marsh harvest mouse (*Reithrodontomys raviventris halicoetes*) lives in the salt marshes surrounding San Francisco Bay and the lower reaches of the Sacramento River. This small rodent (about 11–17 gm.) is restricted to the *Salicornia* marshes and is never found in the uplands (Hooper, 1944).

The ability of the harvest mouse to live in salt marshes suggests that it is able to tolerate ingestion of bay water and/or the salty saps of the plants, primarily the halophilic *Salicornia*. Successful utilization of these fluids would require the harvest mouse to produce urine with salt concentrations similar to those reached in the urine of some desert rodents (Schmidt-Nielsen, 1950; Bartholomew and Hudson, 1959; Hudson, 1962). It might also require adaptations which would negate the cathartic effects of the magnesium and sulfate in sea water, which in man cause diarrhea and thus an increased drain on the water reserves (Wolf, 1958).

In this study we determined (*a*) whether the harvest mouse can successfully drink sea water, (*b*) the effects on body weight of drinking salt solutions of increasing concentrations, and (*c*) the effect of restricted quantities of fresh water.

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MATERIAL AND PROCEDURES

MATERIAL AND ANALYSES

The animals used in the study were trapped in their natural environment and sent to us by Dr. E. W. Jameson, Jr., Department of Zoology, University of California, Davis. Although the animals were not identified to subspecies by comparison with museum specimens, only *R. r. halicoetes* occurs in the area where our animals were trapped (Hall and Kelson, 1959; Hooper, 1944).

The procedures used in the collection and analyses of urine and plasma samples were as follows. The animals were placed in hardware cloth cages over Petri dishes and kept under constant observation. Urine was collected when voided and immediately placed in vials and frozen. Blood was taken from the tail and centrifuged immediately. Plasma was removed from the cells and frozen. Urine and blood samples remained frozen until analysis.

Urea was determined by the method of Conway (1958). Chloride was determined with a Cotlove chloridometer (Laboratory Glass and Instrument Corporation). Total electrolyte concentration was determined by conductivity (Holm-Jensen, 1947) and expressed as the concentration of a sodium chloride solution with the same electrolytic conductivity. A modification of the method of Gross (1954) was used to determine osmolality.

The animals were weighed with an accuracy of 0.1 gm. on a Mettler K7T balance readable to 0.01 gm.

To measure fluid consumption these mice were housed in cylindrical tin cans (14 cm. high, 10 cm. in diameter) rather than standard mouse cages. Each cage was provided with a drinking device that consisted of a reservoir under which was attached a vial partially filled with mineral oil. This vial would catch any fluid spilled during drinking, and evaporation from the spilled fluid was prevented by the oil. The decrease in weight of the entire device during a particular period, corrected for evaporation from the drinking orifice, represented the fluid consumption of the animal. Evaporation from the orifice was measured with a similar drinking unit fitted to an empty cage.

EXPERIMENTAL PLAN

Maintenance of body weight was taken to indicate maintenance of a positive water balance. If body weight decreased continually after a particular solution was given, it was concluded that the solution had either caused an actual loss of water or had caused the animals to decrease their fluid or food consumption.

Utilization of sea water.—The animals were fed on Purina Lab Chow which was available in excess at all times. They were housed either singly or doubly in pan-type mouse cages.

Four animals were given sea water for drinking while three control animals received ad libitum distilled water. The sea water, collected near Wilmington, North Carolina, had a chloride content of 487 mN and a total electrolyte concentration of 540 mN.

During this experiment the temperature varied between 22.8° C. and 34.4° C. and relative humidity averaged 40 per cent.

Tolerance to sodium chloride solutions.—A group of five mice was used to show the effects of salt solutions on body weight. These mice were given NaCl solutions, which were made more concentrated as time progressed. The control group of five animals was given distilled water ad libitum. The fluid consumption was recorded for both groups.

Effect of restricted water supply.—One test group of five animals was used to show the effects of restricted water supply. These animals were given progressively smaller quantities of water. During the first 24 days the ration was a weighed portion of water given to the mice once a day. As these portions became smaller it was difficult to administer them accurately. This problem was solved by substituting weighed pieces of cucumber for water. Cucumber contains 96–97 per cent water and proved to be a convenient and quite accurate method of administering small quantities of water. Water-restricted animals ate the cucumber quickly so that errors from evaporation were insignificant.

The experiments on salt tolerance and restricted water supply were done simultaneously, and thus one control group served for comparison with both experimental groups. The control group received ad libitum distilled water. Fluid consumption was measured in three of these five mice in the same way as in the salt-tolerance group.

During the experiments on salt tolerance and restricted water supply the temperature varied between 20.0° C. and 25.5° C. Average relative humidity, recorded in the mid-morning, was 76 per cent.

RESULTS

SEA WATER AS DRINKING FLUID

The absence of any important difference in body weight between the mice drinking sea water and those drinking distilled water indicated that sea water could be utilized as well as fresh water (Table 1). No diarrhea was observed—

TABLE 1

CHANGES IN BODY WEIGHTS OF HARVEST MICE DRINKING SEA WATER AND FRESH WATER FOR 30 DAYS

Original Weight (Gm.)	Final Weight (Gm.)	Per Cent Original Weight
Sea Water		
14.2	12.2	85.9
14.0	12.0	85.7
13.4	12.0	89.6
13.2	11.4	86.4
Mean.....13.7	11.8	86.9
Fresh Water		
18.9	15.8	83.6
14.7	13.3	90.5
14.7	13.4	91.5
Mean.....16.1	14.2	88.9

the fecal pellets remained firm. No long-term effects were apparent because these mice lived for many months after the experiment.

SALT TOLERANCE

The tolerance to sodium chloride solutions varied from individual to individual (Fig. 1). Weight declined gradually in most of the animals until the 0.7 *N* solution was given on day 22. Following day 22, weight decreased rapidly until day 30 when it stabilized in four of the animals. The noticeable increase in weight between days 34 and 35 was apparently due to increased fluid consumption when the concentration was raised to 0.8 *N*. This response lasted only one day.

The amount of fluid imbibed was measured in three of the five animals (Table 2)—the other two spilled fluid from the wastage tube and thus made the meas-

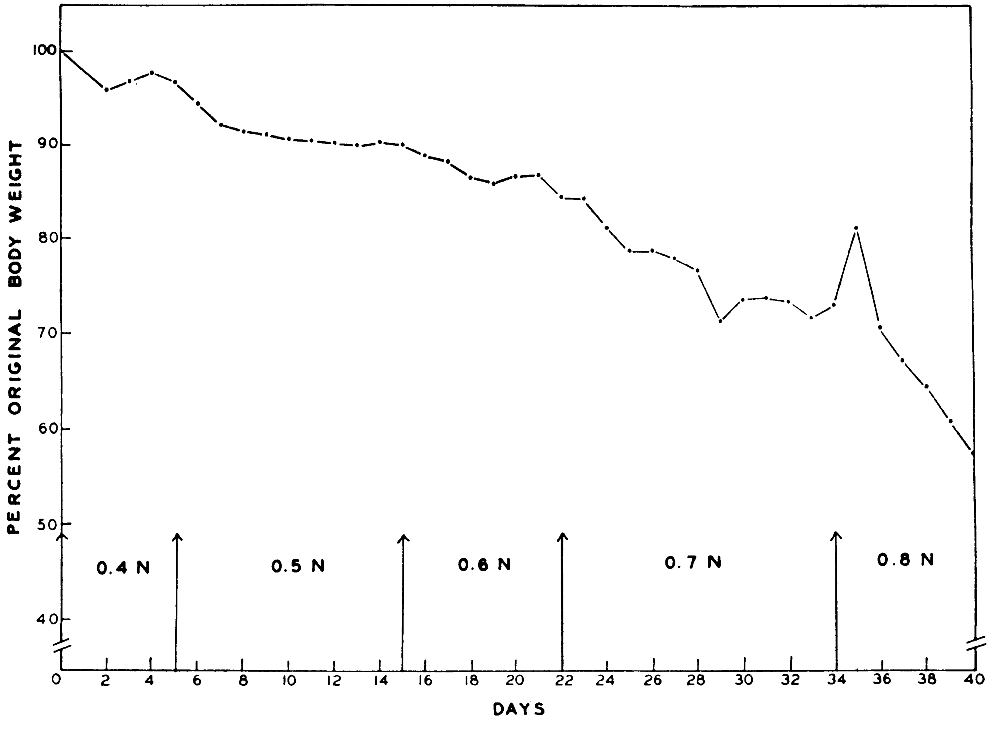

FIG. 1.—Weight changes of salt marsh harvest mice while drinking NaCl solutions. The periods in which particular normalities of NaCl were given are enclosed by vertical arrows. Results of five individuals are averaged here.

urements inaccurate. Comparison of the consumption during day 34 to the average consumption of 0.7 *N* NaCl shows a two- to threefold increase in drinking. After day 34 the animals drank much less or practically stopped drinking, and at the same time there was a rapid decline in weight.

RESTRICTED WATER SUPPLY

While receiving 3 gm. water per day, the mice maintained body weight. Further decrements in water supply were associated with weight loss (Fig. 2). When the water supply was reduced to 2 gm., the body weight decreased rapidly for 3 days but subsequently stabilized at approximately 85 per cent of the original weight. When the water was reduced to 1.5 gm. and then to 1 gm. per day, the weight stabilized at 80 per cent of the original weight. The weight decreases followed by stabilization probably reflect an adjustment or acclimation to the restricted water supply.

Apparently the smallest ration on which weight could be maintained was 0.8 gm. cucumber per day. Sustained weight loss occurred when 0.7 gm. cu-

TABLE 2

MEAN CONSUMPTION OF NACL SOLUTIONS IN FIVE INDIVIDUAL HARVEST MICE IN PER CENT OF BODY WEIGHT PER DAY (± STANDARD DEVIATION)

0.7 *N* NaCl (12 Days)	0.8 *N* NaCl	
	First Day	Remaining 5 Days
19.1±2.29	55.5	3.1±0.82
19.7±9.03	*	5.8±1.72
22.8±7.40	46.1	8.8
14.6±7.66	*	10.4±3.28
26.5±5.13	51.4	12.8±2.14

* Observation invalid.

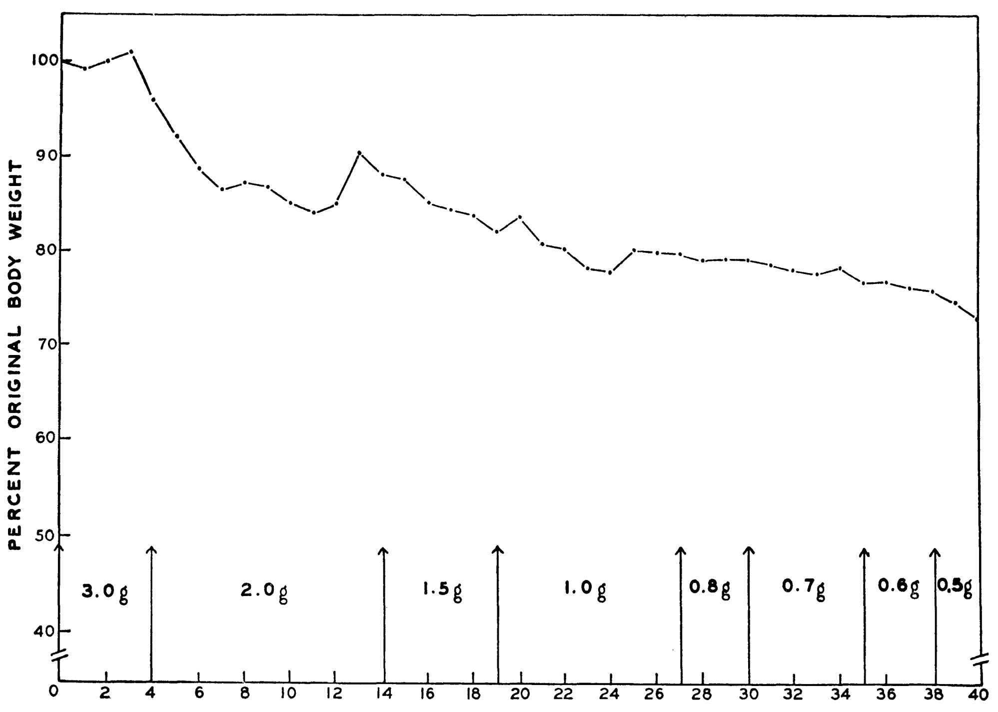

FIG. 2.—Weight changes of salt-marsh harvest mice while receiving limited rations of water. The periods in which particular quantities of water were given are enclosed by vertical arrows, and the weight of the ration is shown as grams per day per animal. Results of five individuals are averaged here.

cumber or less was given, and there was no indication of further weight stabilization.

WEIGHT CHANGES AND WATER CONSUMPTION IN CONTROL MICE

The relative weight of the animals serving as controls for the salt-tolerance and water-restriction experiments changed little during the experiment. The average weight was 98.2 per cent of the original body weight and varied from 103 per cent to 94 per cent with a standard deviation of ±2.28 per cent.

Daily consumption of water was recorded for three of the five control animals (Table 3). The values agree with

TABLE 3

WATER CONSUMPTION IN HARVEST MICE DRINKING DISTILLED WATER AD LIBITUM

Body Weight Gm. (±S.D.)	Water Consumed per Day, Per Cent of Body Weight (±S.D.)	Predicted Water Consumption per Day, Per Cent of Body Weight
14.1±0.04....	14.7±1.91	17.4
11.7±0.05....	23.1±3.58	18.1
13.6±0.06....	18.0±4.88	17.6

predicted values calculated from the heterogonic equation for water intake relative to body size of mammals (Adolph, 1949).

URINE AND PLASMA CONCENTRATIONS

Urine concentration.—The maximum urine osmolality was similar in the two experimental groups (Table 4). The highest osmolality that was observed was 4,180 mOsmolal and was found in the restricted-water group. The same animal also provided the highest osmotic U/P ratio of 12.5.

As was expected, large differences occurred in the concentrations of urea and electrolytes in the urines from the various groups. The highest urea concentration was 1,990 mM and the highest total electrolyte was equivalent to 1,018 mN NaCl. These maximum values were observed in the restricted-water group and the salt-tolerance group, respectively.

Total electrolyte concentrations in the samples from the salt-tolerance group were all well above the concentration of the drinking fluid (0.8 N). However, with one exception (837 mN) the chloride concentration was not. A similar discrepancy between the concentration of the urine and the drinking solution has been observed in kangaroo rats (Schmidt-Nielsen, 1950) where the total electrolyte concentration in the urine was not always

TABLE 4

URINE CONCENTRATIONS IN SALT-MARSH HARVEST MICE

Osmolality (mOsmolal)	Urea (mM)	Electrolytes (mN NaCl)	Chloride (mN)
Salt-Tolerance Group			
3,330	1,550	912	456
3,110	1,460	897	509
3,090	1,460	903	517
2,770	839	1,018	837
1,990	341	871	642
Mean...2,860	1,130	920	592
Restricted-Water Group			
4,180	2,590	670	....
3,680	2,430	653	213
2,760	1,560	470	33
2,700	1,670	508	132
2,520	1,700	457	33
Mean...3,170	1,990	552	103
Control Group			
1,610	980	357	127
1,360	800	278	94
1,060	743	257	....
1,000	584	247	107
915	475	241	134
Mean...1,190	716	276	116

as high as that of the sea water the animals were drinking. However, we have evidence from other observations that the discrepancy is caused by a diuresis which occurs due to disturbance of the animal during the sampling period.

Plasma concentrations.—Plasma urea was slightly elevated in the salt-tolerance group as compared to the concentration found in the restricted-water group and in the control animals (Table 5). Otherwise, notable differences in plasma concentrations were absent.

DISCUSSION

The ability to utilize sea water for drinking is of obvious survival value to the salt-marsh harvest mouse. However, this would not apply directly to other animals that experimentally have been exposed to sea-water drinking (e.g., white rats and kangaroo rats). These latter may never come in contact with sea water in their natural environment and certainly could not depend on it as a water source. Adolph (1944) found that white rats could not maintain weight while drinking sea water. More recently, however, desert rodents have been examined that are able to drink not only sea water but also sodium chloride solutions of higher concentrations than sea water (Hudson, 1962; Winkelmann and Getz, 1962; Schmidt-Nielsen, 1950). The salt-marsh harvest mouse in this study successfully drank sea water (540 mN electrolyte concentration), and the data indicated that they could survive indefinitely while drinking 700 mN NaCl solution.

While diarrhea has occurred in other animals drinking sea water, it was not noticed in the harvest mouse. Apparently this factor is of limited importance in the consumption of sea water in this animal. It appears then that the capacity to utilize sea water for drinking purposes depends primarily on the ability of the kidney to form a concentrated urine.

The kidney of this harvest mouse produces highly concentrated urine with a concentration limit intermediate between the kangaroo rat (*Dipodomys merriami*) and the ground squirrel (*Citellus leucurus*). The maximum urine concentration observed for these three species is 5.5 Osm. for the kangaroo rat, 4.1 Osm. for the harvest mouse, and 3.9 Osm. for the ground squirrel.

The ability of *Reithrodontomys raviventris halicoetes* to utilize sea water for drinking does not prove that it does so in

TABLE 5

PLASMA CONCENTRATIONS IN SALT-MARSH HARVEST MICE

Osmolality (mOsmolal)	Urea (mM)	Electrolytes (mN NaCl)	Chloride (mN)
Salt-Tolerance Group			
363	21.2	167	118
363	9.9	165	130
332	20.6	155	108
305	17.0	152	116
269	11.1	137	96
Mean...326	16.0	155	114
Restricted-Water Group			
377	....	....	93
335	11.1	150	112
322	9.4	155	110
312	9.2	155	107
312	6.8	147	106
Mean...332	9.1	152	106
Control Group			
335	9.2	147	110
332	10.2	150	114
327	7.0	154	111
326	11.1	155	109
311	8.2	154	118
Mean...326	9.1	152	112

its natural environment. The animals in this study were able to maintain a stable although reduced body weight while receiving approximately 0.8 gm. fresh water per day. Appreciable dew deposition should occur in salt marshes near the ocean, and it seems possible that 0.8 gm. of water per day could be available from this source. In either case, whether the animal drinks sea water or limited quantities of fresh water, the kidney apparently functions with equal efficiency. This was indicated by similar urine concentrations produced in the salt-tolerance group and in the restricted-water group.

SUMMARY

The salt-marsh harvest mouse (*Reithrodontomys raviventris halicoetes*) lives only in salt marshes. This suggests an ability to tolerate sea water and/or the salty saps of marsh plants. It was found that these harvest mice could, in fact, drink sea water (540 mN electrolytes) and maintain body weight with no evidence of diarrhea. NaCl solutions were used to test the salt tolerance of these animals; the highest concentration that was utilized successfully was 700 mN.

When fresh water was available the harvest mice drank approximately 19 per cent of the body weight per day, or 2.4 gm. per day. However, when water consumption was restricted, 0.8 gm. cucumber (96–97 per cent water) per day provided enough water.

The experimental conditions caused the formation of maximally concentrated urine. The highest values observed were 4,180 mOsmolal, 2,590 mM urea, and 1,018 mN electrolytes.

The significance of these findings in the ecology of the harvest mouse is discussed.

ADDENDUM

After the acceptance of this manuscript, Fisler (*Ecology*, **44**:604–8, 1963) published data showing that *Reithrodontomys raviventris halicoetes* could make use of sea water whereas *R. r. raviventris* and *Reithrodontomys megalotis* could not. The present study confirms Fisler's findings in respect to *R. r. halicoetes*. It provides additional information on weight changes in this animal while drinking NaCl solutions or small quantities of fresh water and reports plasma and urine concentrations.

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