Effects of Salt Water on Food and Water Consumption and Weight of Harvest Mice
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Source: *Ecology*, Vol. 44, No. 3 (Jul., 1963), pp. 604-608
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/1932549
Accessed: 27-03-2015 07:37 UTC

TABLE IV. Average survival time in minutes ± standard error of groups of termites

Caste	Species	N	Average survival time	σ
STILL AIR				
Workers	*tibialis*	4	690±51.96	103.92
	flavipes	4	435±70.85	141.7
	arenincola	4	405±82.61	165.23
	virginicus	4	330±51.95	130.92
2d form sexuals, nymphs	*tibialis*	4	855±15	30.0
	virginicus	4	645±45	90.0
	arenincola	4	540±81.24	162.48
	flavipes	4	375±78.8	157.7
MOVING AIR				
Workers	*flavipes*	8	255±18.8	53.2
	virginicus	20	291±26.9	120.4
Soldiers	*flavipes*	8	255±18.81	53.2
Nymphs	*flavipes*	16	300± 9.49	37.95
2d form Sexuals	*virginicus*	8	307±17.71	50.09
Imagoes teneral 3-days flight cond.	*flavipes*	12	275± 8.92	30.92
	flavipes	12	350±10.68	37.01
	virginicus	32	270± 7.62	43.13

SUMMARY

Eastern species of genus *Reticulitermes* include the rather desiccation-tolerant *tibialis,* which loses water at a consistently low rate, 3 species that lose water relatively slowly but show great variability under experimental conditions, and a species, *flavipes,* that shows a variable but relatively high rate of water loss. The desiccation tolerance of *tibialis* appears to be associated with a relatively effective waterproofing mechanism, a well-developed cement layer, and moderate size. *R. flavipes* seems to have the least efficient transpiration-retarding mechanism, and the fact that samples of this species may outlive samples of species having lower loss rates during experimental drying is probably owing to its large size.

Transpiration resistance increases with age, in the absence of damage, as does resistance of the waterproofing to damage from peanut oil. This results in the rate of transpiration in imagoes falling to about one-third the rate of teneral individuals.

Size appears to have no influence on rate of loss though it can influence length of survival under dry conditions.

When treated to demonstrate the cement layer, species of *Reticulitermes* other than *tibialis* were found to have very small argentaffin granules in depressed areas, instead of the heavy scaly layer found in *tibialis.* Futher study of this layer is projected.

ACKNOWLEDGMENTS

The authors wish to express appreciation to Dr. and Mrs. Alfred Emerson and to termite students of the University of Chicago for aid in securing colonies of *tibialis* and *arenincola;* to Dr. Edwin Cook, Dr. Narayan Patel, and Ronald Taylor of the Entomology Department at the University of Minnesota for the loan of equipment and Carbowax, and for many helpful suggestions; and to Dr. L. W. Rees of the School of Forestry for preparing wood for the culture media. H. L. Collins deserves special gratitude for making the work of one of us (MSC) possible, and for collecting many colonies of the Florida species used in the study.

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EFFECTS OF SALT WATER ON FOOD AND WATER CONSUMPTION AND WEIGHT OF HARVEST MICE

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The study of the effect of salt water consumption on the weight, drinking, and survival of small mammals has been concerned primarily with experimentation with desert dwellers which may have a problem in water conservation. High concentrating ability in the kidneys of these mammals may allow successful and efficient use of sea water for drinking. The existence of a species of harvest mouse, *Reithrodontomys raviventris,* which is essentially restricted to the salt and brackish marshes of San Francisco and related bays in California, offers an unusual opportunity to study this subject in an animal which presumably could have adapted to salt-water drinking *per se.* The harvest mice of the San Francisco Bay marshes were originally described as 2 species, *Reithrodontomys raviventris* (Dixon 1908), and *R. halicoetes* (Dixon 1909). Later works regarded the 2 forms as conspecific (Howell

1914; Hooper 1944; Hall and Kelson 1959). This latter relationship has recently been verified by studies of the morphology, ecology, physiology, and behavior of the forms involved (Fisler MS). The 3d form present in the San Francisco Bay region is *R. megalotis longicaudus*, a primarily grassland species which also inhabits the edges of salt and brackish marshes, as well as fresh-water marshes. It is the purpose of this report to describe certain characteristics of these 3 kinds of harvest mice with regard to normal food and water ingestion, dehydration, and the effect of drinking salt-water solutions on weight and food and water consumption.

Methods

Animals were housed individually in hardware-cloth cages. Food and water was provided *ad libitum* to all animals except those which were being dehydrated. These latter had food available to them at all times. Test tubes with the open end partly closed to prevent leakage were used to supply water. These were attached securely to the cages so that excessive jarring by a mouse would not cause undue spillage. Similar test tubes placed near the cages were used to correct for evaporation. Weights of the mice, fluid levels in the test tubes, and the weight of the unconsumed food pellets were checked daily, at about 8:00 AM as a rule, but occasionally at 11:00 AM. In either case, the mice had ceased the activities of the night before recording these measurements. The environmental conditions of the laboratory were not appreciably different from the natural situation in temperature and humidity.

The food used was a standard laboratory ration known as Diablo animal chow. Two or 3 of these dry pellets were always in the cage with the mouse. These were occasionally chewed by the mouse and not completely consumed, but this was easily detected and the record for consumption on that day deleted. Some waste was inevitable, but by keeping the cages on clean surfaces it was possible to ascertain this and correct for it.

Sea water from the Pacific was used (about 0.57 molar solution) as well as NaCl solutions of 1.0 and 1.5 molar concentrations. Tests using both sea water and salt water of the same concentration did not reveal any gross differences in the reactions of the mice, although sea water and NaCl solutions are not osmotically equivalent drinking fluids.

The majority of animals were taken from salt and brackish marshes near Martinez and Richmond, Contra Costa County, California. Females were in nonbreeding condition, but some of the males were sexually active. No differences in reactions to the various water diets were noted between the sexes.

Results

Previous findings.—In brief, the following are the known characteristics of salt-water drinking for the 3 harvest mice studied here (Fisler MS). In preference tests between fresh water and various concentrations of salt water, it had been found that *R. m. longicaudus* greatly preferred fresh water but that a few individuals could tolerate some salt water in their diet and actually chose it. There was no essential difference between individuals from grassland or marsh areas. *R. r. raviventris* preferred some salt in its diet, but it could not survive on sea water or on salt water of higher concentrations. *R. r. halicoetes,* though actually preferring to drink fresh water, could survive for extended periods (up to at least 395 days) on sea water, but not on the higher concentrations used in these experiments (1.0 and 1.5 molar NaCl). Data regarding initial and final weights and the length of life during dehydration and while drinking various concentrations of salt water have been summarized in Table I. These data show that both *megalotis* and the subspecies *raviventris* could live longer while drinking sea water than they could while being dehydrated whereas this was not possible while using salt water of higher concentrations. *Halicoetes* could survive on sea water but not on the higher concentrations of salt water, and at a concentration of 1.0 mole life was not greatly extended beyond the length of life while being dehydrated. The length of life was actually shortened at the 1.5 molar concentration.

TABLE I. Comparison of weight with the length of life under various conditions of drinking (Data from Fisler, MS)

Form	N	Initial weight; mean and range	Weight at death; mean and range	Length of life; mean and range
Dehydration				
megalotis	15	9.8 g 8.3-13.7	5.7 g 5.3-6.7	3.9 days 2-7
raviventris	15	10.0 8.2-13.6	6.2 5.0-7.7	4.2 2-12
halicoetes	20	12.4 8.5-17.6	6.1 5.1-6.8	8.6 3-15
Sea water (0.57 mole)				
megalotis	12	10.0 7.7-12.4	5.8 4.9-7.1	19.7 3-72
raviventris	12	10.1 7.2-14.0	6.5 4.5-9.1	12.0 3-48
halicoetes	12	13.8 10.6-16.2	[a]	200.6[a] 29-395
1.0 molar NaCl				
megalotis	11	9.2 7.4-12.0	6.2 4.9-7.9	2.7 1-5
raviventris	10	11.2 7.3-14.1	6.3 5.7-7.2	3.6 2-7
halicoetes	11	12.7 8.6-18.2	6.7 5.8-8.0	10.7 2-27
1.5 molar NaCl				
megalotis	3	8.3 7.7- 8.7	5.7 5.3-6.1	2.3 2-3
halicoetes	6	12.1 9.6-14.5	6.9 6.1-9.3	6.3 4-9

[a] Many *halicoetes* were still alive at the end of the test period.

Weight loss.—All animals lost weight at varying rates under the conditions imposed, that is, dehydration or the drinking of the 3 different concentrations of salt water. The average percentage weight loss (Table II) during the period from the introduction of the condition until death or removal to standard conditions varied with the initial weight of the mouse, as did the length of life; that is, the greater the initial weight, the greater the weight loss and the longer the survival of the animal.

The average weight lost per day shows that the animals lost less weight per day while drinking sea water than while dehydrating (Table II). The rates here for *megalotis* and the subspecies *raviventris* were comparable. However, the rates for these 2 forms at higher concen-

TABLE II. Comparison of weight loss

Form	N	% weight lost; mean and range	Weight lost per day; mean and range
Dehydration			
megalotis	15	40.7 31.3-56.9	1.07 gms. 0.77-1.30
raviventris	15	37.8 27.4-58.1	1.01 0.66-1.45
halicoetes	20	49.1 28.6-63.1	0.74 0.59-0.95
Sea water (0.57 mole)			
megalotis	12	41.1 30.4-53.2	0.58 0.05-1.50
raviventris	12	34.9 17.4-55.7	0.60 0.11-1.43
halicoetes	12	45.0 24.4-57.3	0.073 0.008-0.245
1.0 molar NaC1			
megalotis	11	32.2 17.6-43.3	1.13 0.80-1.37
raviventris	10	40.4 23.1-56.5	1.34 0.74-2.40
halicoetes	11	45.8 25.6-61.5	0.66 0.35-1.10
1.5 molar NaC1			
megalotis	3	31.7 29.9-34.1	1.16 0.97-1.30
halicoetes	6	42.9 32.3-54.1	0.82 0.78-0.88

TABLE III. Normal drinking and food consumption

Form	N of individuals	N of records	Weight; mean and range	Mean fresh water drunk cc/g/day
WATER				
megalotis	8	30	9.5 gms. 8.0-11.6	0.325
raviventris	6	26	10.3 8.3-11.5	0.218
halicoetes	9	33	11.9 9.8-15.5	0.229
FOOD				Mean food eaten, g/g/day
megalotis	9	33	9.8 8.0-11.6	0.258
raviventris	6	26	10.3 8.3-11.5	0.245
halicoetes	9	33	11.5 9.8-13.5	0.227

trations of drinking fluid rose considerably above the rates while drinking sea water. For *megalotis,* the rate of weight loss at the 1.0 molar concentration was about the same as that for dehydration, but the animals died more quickly and so lost less total weight. For the subspecies *raviventris,* the rate at 1.0 mole was much higher than during dehydration, and the total weight lost was slightly higher, although the animals died about one-half day sooner at the 1.0 molar level.

The situation for *halicoetes* was considerably different (Table II). The rate for dehydration was much lower though the weight loss percentage was greater than for either *megalotis* or *raviventris.* The rate while drinking sea water was very low. On sea water, the weight of an individual of *halicoetes* fell very slowly, almost imperceptibly, until, apparently, there was no excess fat remaining. After this, the animals continued living at a reduced weight. *Halicoetes* was able to live on the 1.0 molar concentration of salt water 3 or 4 times as long as could either *megalotis* or *raviventris.* Consequently, its percentage weight loss was higher than for either *megalotis* or *raviventris,* whereas its rate of weight loss was only one-half that of the other 2 forms.

The weight loss per day given in Table II is an average figure for the entire period while the individual animal was being subjected to a particular condition. These individuals varied considerably in their pattern of weight loss, but, in general, weight loss was higher when first placed on a fluid and lower near the time of death. However, this was not always the case, and sometimes absolute weight losses were higher during the last day or 2 of life than earlier. There was never any gain in weight by individuals of *megalotis,* of the subspecies *raviventris,* or of the subspecies *halicoetes* when the latter was dehydrated or was drinking 1.0 or 1.5 molar salt solutions. Individuals of *halicoetes* drinking sea water, however, did have long periods when they actually gained weight. Weights fluctuated considerably but essentially finally reduced to a more or less fat-free weight (6.5 to 10.0 g, depending on the body size of the individual). Mice autopsied after death and those removed from the sea-water regimen had little or no macroscopically visible subcutaneous or mesenteric fat.

Normal drinking and food consumption.—Normal consumption of fresh water and food was measured (Table III) to compare with the data from the abnormal conditions. Averages were computed on the basis of cm^3 drunk or g eaten per g of body weight per day. It was found that *raviventris* and *halicoetes* drank about the same amounts of fresh water but that *raviventris* ate slightly more per g of body weight. *Megalotis,* on the other hand, drank considerably more per g of body weight than did either *raviventris* or *halicoetes* and ate slightly more than either, on the average. Variations between individuals was, of course, frequent, but it did not appear to be related to any common factor. Heavy mice ate and drank either more or less than average without any consistency. This was also true of lighter individuals. Consumption by any one individual varied but was less than the variation between individuals.

Effects of salt water.—Consumption of sea water as the only drinking fluid decreased the amount of fluid intake to 89.8% of normal in *megalotis* and to 83.0% of normal in *halicoetes* (Table IV). It would seem inconsistent that the amount of drinking should be reduced more for *halicoetes* than for *megalotis,* but this may be related to a lesser concentrating ability in the *megalotis* kidney which may have required more water than did *halicoetes* to eliminate the excess salt (assuming that the salt is excreted). Of course this only added more salt to the diet and perhaps hastened the death of these

TABLE IV. Effect of drinking salt-water solutions on the ingestion of food and water

	WATER					FOOD				
Form	N of individuals	N of records	Weight, mean[a] and range	Mean water drunk, cc/g/day	% of normal consumption	N of individuals	N of records	Weight, mean[a] and range	Mean food eaten, g/g/day	% of normal consumption
Sea water (0.57 mole)										
megalotis	8	84	8.2 gms. 6.9-9.3	0.292	89.8	7	82	8.2 gms. 6.9-9.3	0.216	83.7
raviventris	3	21	7.2 6.0-8.7	0.185	84.9	12	113	8.3 6.0-10.8	0.163	66.5
halicoetes	6	67	11.8 10.6-13.6	0.190	83.0	8	91	11.7 10.6-13.6	0.219	96.5
1.0 molar NaC1										
megalotis	11	30	7.7 6.4-10.0	0.080	24.6	11	30	7.7 6.4-10.0	0.083	32.2
raviventris	10	36	7.8 6.3-8.9	0.095	43.6	10	36	7.8 6.3-8.9	0.110	44.9
halicoetes	6	46	9.2 8.4-10.5	0.083	36.2	6	50	9.2 8.4-10.5	0.125	55.1
1.5 molar NaC1										
megalotis	3	7	7.0 6.5-7.4	0.058	17.8	3	7	7.0 6.5-7.4	0.125	48.4
halicoetes	2	13	9.0 9.0,9.1	0.048	21.0	2	13	9.0 9.0,9.1	0.068	30.0

[a] Mean of mean weight of each individual during the period spent drinking each concentration of salt water.

animals. *Halicoetes,* on the other hand, maintained itself on this lesser amount of water.

Food consumption by *halicoetes* was reduced only 3.5%. This undoubtedly allowed the animals to maintain themselves for long periods of time (see Table I), but did not allow accumulation or retention of fat during this period. *Raviventris* food consumption was reduced to 66.5% of normal and so these animals died relatively quickly (average, 12 days; see Table I). *Megalotis,* consuming about 84% of normal food requirements, was longer lived while drinking sea water than was the subspecies *raviventris* (average, 19.7 days), and the reason here seems to lie in the greater food consumption by *megalotis.* It is difficult to ascertain whether these 2 forms were dying of slow starvation, some sort of "salt poisoning," or dehydration. Since starvation occurs rather quickly in all 3 forms when no food is provided (2 to 6 days, dependent on initial weight), and the weight loss usually is not as great as during dehydration or drinking salt fluids, one is inclined to the view that death is due to a form of "salt poisoning" or to dehydration.

Mice placed on the 1.0 molar NaCl solutions all reduced their food and water intake to less than 50% of normal with the exception of the food consumption by *halicoetes* which ate at a rate of 55.1% of normal (Table IV). The form that consumed food at a rate closest to its normal intake lived the longest, although this same form (*halicoetes*) also tolerated the drinking of salt-water solutions better than did the other 2 forms.

Only *megalotis* and *halicoetes* were tested on the 1.5 molar NaCl solution. The reactions here were presumably an intensification of those at the 1.0 molar solution with the exception that *megalotis* consumed 48.4% of normal food requirements (Table IV). One would suspect from other results here that this percentage should be something like 30 or 35. This discrepancy was due to one individual which ate near normal amounts for 2 of the 7 days recorded. The 5 records available for the other 2 individuals showed a food consumption of 38% of normal.

Exceptional individuals.—Two individuals of *megalotis* on the sea-water regimen lived much longer than the average for this species. The food and water consumption of these 2 individuals was measured both at the beginning and at the end of the test period. One mouse lived for 60 days and drank at a rate that was 42.5% of its normal consumption at first, but later the rate rose to 217.8% of normal. In total, it drank at 85.2% of normal. Food consumption in this individual was lessened at first (64% of normal) and greater near death (79.8% of normal). In all, this mouse ate food at a rate of 70.9% of its normal rate. The 2d *megalotis,* which lived 72 days on sea water, reacted quite differently. At first it drank at 112.9% of normal but later only at 78.8% of its own normal rate. All told, it drank at a rate of 94.8% of its normal consumption. Its eating habits showed consumption at 116.3% of normal at first but 95% later and, all told, 105.4% of normal. In spite of these differences, these 2 mice, of comparable size and weight, lost weight at about the same rate. Such figures as these indicate highly different reactions and requirements between these 2 individuals, both of which were trapped at the same locality on the same day.

Two individuals of the subspecies *raviventris* lived much beyond the average while on the sea-water regimen. These animals lived for 37 and 48 days and consumed food at 82 and 79.6% of their normal rates, respectively. This compares with the average of 66.5% of normal for the form as a whole. No other individuals approached this high level of food consumption while on a salt-water regimen.

Discussion

Two small mammals are known which can effectively utilize sea water and maintain their weight, the Merriam kangaroo rat, *Dipodomys merriami* (Schmidt-Nielsen and Schmidt-Nielsen 1950) and the antelope ground squirrel, *Citellus leucurus* (Bartholomew and Hudson 1959). Both species can maintain weight on salt solutions at least as strong as sea water. Both are desert species and hence adaptation to salt-water drinking is probably a matter of water conservation through an increased concentrating ability of the kidney rather than through a direct adaptation to high salt concentrations. In contrast, the one subspecies which was here shown to be capable of living on sea water (*R. r. halicoetes*) was unable to maintain its normal field weight. Perhaps these harvest mice exist under less rigorous conditions than do desert dwellers. Selection of individuals with a high toleration of salt in their diet, perhaps through the greater concentrating ability of the kidney, would apparently be weaker here than in desert dwellers for the water conservation problem in the San Francisco Bay area marshes is probably not so acute. Instead, the adaptation to salt tolerance, rather than any adaptation for water conservation, may be the main factor involved here.

An alternative hypothesis in explanation of this adaptation is also available. Since adaptation to drinking salt solutions has not been as extensive, nor carried to the degree to which this has been taken in desert species studied, it is possible that desert animals have been subjected to this selection far longer than have the harvest mice of the San Francisco Bay marshes. *R. r. halicoetes* probably developed in isolated marshes in San Francisco and San Pablo bays where salinities varied from fresh, through brackish, to salt water. In view of the geologic history of the filling of the bays, it is quite likely that *R. r. halicoetes* has been in existence less than 25,000 years (Fisler MS). *Dipodomys merriami,* on the other hand, probably originated in the early or middle Pleistocene (Lidicker 1960:206) from a progenitor already adapted to desert living. If these estimates are correct, this kangaroo rat has been subjected to selection for its high kidney efficiency much longer than the salt-marsh harvest mouse has been under selection for high salt toleration.

It is of great interest to note that an ability to drink sea water can be seen in a very limited way in individuals of a grassland form of mouse, *R. m. longicaudus,* and that this characteristic apparently has been further developed in the marshland derivative of this upland species. It is of further interest that the marshland forms have modified this ability in 2 different ways, neither of which as yet represents as good an adjustment to drinking sea water as has been attained in the desert species of rodents studied thus far.

Summary

The restriction of the harvest mouse *Reithrodontomys raviventris* to salt and brackish marshes of the San Francisco Bay region raises the question of whether it has the ability to use salt water as drinking water. A 2d species, *R. megalotis,* lives in grasslands and in the edges of these marshes. The effect of salt-water solutions on weight and food and water consumption was investigated in these species.

All animals lost weight while being dehydrated or while drinking sea water or sodium chloride solutions of 1.0 and 1.5 molar concentrations. However, one of the 2 subspecies of *raviventris* was able to survive for more than one year on sea water although at a minimum weight level. This form (*halicoetes*) also tolerated higher concentrations of salt water in its diet as well as dehydration better than did the other 2 forms studied, but none of these mice could survive for long periods under these conditions. Food and water consumption was greatly curtailed while drinking sea water.

Certain desert species of small mammals can drink sea water, but this seems to have arisen in connection with an increased concentrating ability in the kidney for water conservation rather than for toleration of excessive salt as seems to be the case in the harvest mouse studied here. Desert and salt-marsh mice have apparently each met a different problem in a similar manner.

The ability to drink sea water for long periods of time exists in one marsh subspecies but not in a 2d subspecies of the same species. Two slightly different environments have been adjusted to in different ways by one species of mouse.

These experiments on salt-water relationships were partly supported by a National Science Foundation Summer Fellowship for 1959. Various facilities and materials were supplied by the Museum of Vertebrate Zoology and the Department of Zoology of the University of California, Berkeley. The project was under the supervision of Dr. Alden H. Miller.

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