

THE WATER ECONOMY OF THE SAGE SPARROW, *AMPHISPIZA BELLI NEVADENSIS*

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The water balance of desert birds has only recently received intense study. Chew (1961), Bartholomew and Cade (1963), Cade (1964), Schmidt-Nielsen (1964), and Dawson and Bartholomew (1968) have reviewed the early literature on the subject, and, based on these early works, the ecological and evolutionary aspects of avian water economy in deserts have been discussed (see, e.g., Bartholomew and Cade 1963). In general, it appears that most species are dependent on surface water or succulent foods to satisfy their physiological requirements for water. However, more recent investigations have shown that certain desert species are sufficiently able to reduce water losses to survive long periods on a dry diet of seeds without drinking. These species include the Budgerygah, *Melopsittacus undulatus* (Cade and Dybas 1962), and the Zebra Finch, *Taeniopygia castanotis* (Calder 1964; Cade et al. 1965), of Australia; the Cutthroat Finch, *Amadina fasciata* (Edmonds 1968); Stark's Lark, *Spizocorys starki*, and the Grey-backed Finch-Lark, *Eremopterix verticalis* (Willoughby 1968), of Africa.

Of the North American desert species investigated, only the Black-throated Sparrow, *Amphispiza bilineata*, has such capabilities.² It can survive indefinitely either without water or on 0.40 M NaCl drinking solution, and measurements of urine Cl⁻ concentrations indicate levels higher than for most avian species (Smyth and Bartholomew 1966a). The Black-throated Sparrow inhabits some of the most extreme desert conditions in North America, breeding in sagebrush and creosote bush deserts from northeast California and southwest Wyoming south to northern México.

The Sage Sparrow, *Amphispiza belli*, which is the only congener of the Black-throated Sparrow, inhabits similar desert region. One subspecies, *A. belli nevadensis*, has a breeding

distribution somewhat more northerly than the Black-throated Sparrow, extending from the high sagebrush deserts of eastern Washington south through eastern Oregon and southwestern Idaho to southern Nevada and northern Arizona (A.O.U. 1957). The breeding ranges of the two species broadly overlap in Nevada. Both species are considered granivorous and commonly occur far from surface water. Because of the similarities in distribution, habitat, and diet of these two closely-related species, a comparison of their water economies may provide further insight into the patterns of avian water economy in desert environments. This study provides an analysis of several physiological aspects of the water economy of the Sage Sparrow.

METHODS AND MATERIALS

EXPERIMENTAL ANIMALS

Of 35 Sage Sparrows used in this study, 27 were captured with Japanese mist nets during the summers of 1967 and 1968 in the vicinity of Cabin Lake Guard Station, 9 mi. N of Fort Rock, Lake County, Oregon, and eight were collected in a similar manner near Unionville, Humboldt County, Nevada, in November 1966. At the time of capture, the birds were weighed to the nearest 0.1 g with an Ohaus triple beam balance. The birds were transported to Oregon State University where all laboratory tests were conducted. An additional 47 birds were shot in the vicinity of Fort Rock between April 1967 and April 1968 for information on body weight and stomach contents.

MAINTENANCE

Except during salt water discrimination tests, all birds were housed individually in small cages (22 × 24 × 41 cm) located in a windowless room with a 12-hr photoperiod (09:45–21:45). Room temperatures generally remained constant at 20°C but occasionally fluctuated from 18.5 to 22°C. Humidity was not controlled and varied between 10 and 30 per cent. Although the birds remained in excellent condition on a diet of only vitamin-enriched chick-starter mash, they were occasionally given millet seed, freshly-chopped lettuce and *Tenebrio* larvae. Unless otherwise stated, only the chick-starter mash was used during actual experimentation. Water was provided ad libitum. The birds were weighed to the nearest 0.1 g with a Mettler top loading balance or an Ohaus triple beam balance either daily or every other day, at the end of the dark period.

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² Ohmart and Smith (Auk, in press) have recently shown that the Brewer's Sparrow, *Spizella breweri*, is also capable of surviving long periods on a dry diet without drinking.

WATER CONSUMPTION

Tap water consumption was measured with inverted 25-ml graduated cylinders fitted with L-shaped drinking tubes similar to those described by Bartholomew and Dawson (1954). Two control drinking devices were used to measure evaporation.

WATER DEPRIVATION

The ability of Sage Sparrows to survive without drinking was investigated using six well-hydrated birds which were deprived of water and provided with only a dry diet of mash (ca. 9.0 per cent water) until death or near death. In order to ascertain the effects of water deprivation on food consumption and activity, the total energy intake and perch activity of six additional birds were measured for five days prior to water deprivation and during four days of water deprivation. Daily gross energy intake was determined by measuring the difference in the dry weight of the food provided at the start of the photoperiod and that remaining at the end of the 24-hr cycle plus any spillage, which was separated from the fecal droppings. Aluminium trays with sides 12.5 cm high placed under the cages were used to catch any spilled food. The mash (mean caloric value = 3.944 kcal/g dry wt) was equilibrated to room moisture conditions, and samples were taken for moisture determinations prior to each feeding. The residual food was dried at 98°C for 24 hr prior to weighing. All weighings were made to the nearest 0.05 g with a Mettler top loading balance. The motor activity of each bird was registered on an Esterline-Angus event recorder each time the bird depressed a mechanical perch located transversely in the cage.

UTILIZATION OF SUCCULENT FOODS

In order to determine the ability of Sage Sparrows to utilize succulent foods as a water source, two groups of birds ($n = 6$ and 10 , respectively) were deprived of drinking water and given lettuce (95 per cent water) or *Tenebrio* larvae (60 per cent water) along with the regular mash diet. Approximately 15 g of freshly-chopped lettuce or about 40 *Tenebrio* larvae were provided each day. Each group was maintained on this regime for at least six days.

SALT WATER UTILIZATION

Sodium chloride drinking solutions were used to ascertain the ability of Sage Sparrows to utilize saline water and to test its effect on the ionic and osmotic composition of the blood and urine. Three concentrations were used: 0.20, 0.25, and 0.30 M. Each concentration was administered after a period of at least seven days on ad libitum tap water. Except for 0.30 M NaCl, which was given for at least four days, each concentration was administered for at least eight days. Fluid consumption was monitored with inverted graduated cylinder drinking devices. Urine samples were collected on the last day of administration of the drinking solution (except for birds on 0.30 M NaCl, from which collections were made on the fourth day).

Following the last day of testing, blood samples were collected with heparinized micro blood collecting tubes after decapitation or after cutting the jugular vein. Care was taken not to cut through the trachea or esophagus. Urine was collected by placing trays of mineral oil (1 cm deep) beneath each cage for a 24-hr period, after which a 50–100 microliter sample was drawn up with blood collecting tubes attached to a 1-ml syringe. Generally several droppings for each bird were pooled. The collecting tubes were

immediately melted shut at one end and centrifuged for 3–5 min at 5000 rpm. The plasma was separated by cutting through the collecting tube at the boundary between the clear plasma and the packed red blood cells. The urine was separated from any oil and uric acid residue in a similar manner. Both the plasma and urine samples were transferred individually to capped microfuge tubes and frozen or stored at 4°C until analyzed. Osmolar concentrations were determined with a Mechrolab Vapor Pressure Osmometer. An Aminco-Cotlove Chloride Titrator was used for Cl⁻ determinations and a Coleman Flame Photometer was used for determinations of Na⁺ and K⁺.

Salt water discrimination tests were carried out with groups of four or five birds in a circular cage (61 cm diam × 61 cm high) made of one-half inch hardware cloth. Four drinking devices were located outside the cage at 90° intervals to one another. The two solutions to be tested were placed in drinking devices opposite one another. Each day at the end of the dark period the drinking devices were rotated 90°. Measurements were taken for at least six days. Four NaCl concentrations were tested: 0.1, 0.15, 0.20, and 0.30 M.

ESTIMATES OF METABOLIZABLE ENERGY AND EXCRETORY WATER LOSS

Estimates of metabolizable energy intake and excretory water loss were made under three regimens of fresh water intake: ad libitum, restricted (2.0 ml/day), and no drinking water but with *Tenebrio* larvae supplied (40 larvae/day). Metabolizable energy was taken as the gross energy intake minus the excretory energy output (see King 1961). The daily gross energy intake was determined, as previously described, for each group for at least five days. Excretory energy was determined for each bird from caloric measurements of two or three pooled 24-hr collections of fecal material. Collections were made from cages fitted with metal perches, one-half inch hardware cloth floors, and cork legs about 1.9 cm long. Voided fecal material was collected on a sheet of preweighed aluminum foil beneath each cage. The cages and foil were located on aluminum trays to contain the dried fecal droppings and spilled food. At the end of each 24-hr period, the foil, wire mesh floor, perches and the trays were removed and replaced. The fecal material adhering to the floor and perches was scraped free and combined with the loose fecal material separated from the spilled mash and not adhering to the foil. The gathered fecal droppings and the foil were dried for 24 hr at 98°C and then weighed with a Mettler analytical balance to the nearest 0.1 mg. A slightly modified method was used for the birds on a regimen of *Tenebrio* larvae and no drinking water. Since the *Tenebrio* larvae frequently dropped through the wire mesh floor and out of reach of the bird, a piece of sheet metal was used in the bottom of the original cleaning tray of each cage. When a collection was made, the sheet metal was removed and the adhering material scraped free with a razor blade. The caloric values for three samples of the chick mash used in this aspect of the study were: 4.170, 4.204, and 4.178 kcal/g dry wt. The mean caloric value for the *Tenebrio* larvae (6.579 kcal/g dry wt) was taken from a published list of caloric values of organisms (University of Pittsburgh, Pymatuning Laboratory of Ecology 1966).

Estimates of daily cloacal water loss were made from the daily weight of the excrement and the per cent water content of individual fecal droppings determined from the wet and dry weights of freshly

TABLE 1. Summary of the field body weights of 77 Sage Sparrows.

	Adults	Immatures	Adults and immatures
Males (n)	26	24	50
$\bar{x}g \pm SE$	18.4 ± 0.24	18.7 ± 0.27	18.5 ± 0.18
range	16.4-20.2	15.9-21.9	15.9-21.9
Females (n)	7	20	27
$\bar{x}g \pm SE$	17.3 ± 0.56	17.8 ± 0.36	17.7 ± 0.30
range	16.2-19.8	15.8-20.9	15.8-20.9

voided material collected on preweighed pieces of aluminum foil placed beneath the cage. The droppings were weighed to the nearest 0.1 mg with a Roller-Smith torsion balance, usually within a half minute after being voided. The droppings were then dried for 24 hr at 98°C and weighed again to obtain the dry weight. Determinations of moisture content of individual droppings were made for the three groups of birds on differing regimes of water intake and for three birds deprived of water for 36 hr.

RESULTS

BODY WEIGHT

The body weights of 77 Sage Sparrows were measured in the field shortly after collection (table 1). The birds were collected at various times during the day from April to October, but no attempt was made to categorize the weights as to time of day or season collected. Immature birds were collected between 15 July and 5 October and aged by plumage characteristics or degree of skull ossification. Male birds averaged nearly a gram more than the females for both adults and immatures, but the means do not differ at the 0.01 level of significance (*t*-test).

WATER CONSUMPTION

The ad libitum consumption of tap water by Sage Sparrows in captivity was highly variable, especially after the birds were housed in small cages for a short time. The mean water consumption by 12 birds maintained on a dry diet of chick mash was 49.3 per cent of the body weight per day (range = 12.7-99.4 per cent, $SE = 6.5$). This mean value is about twice that predicted from the water consumption curve presented by Bartholomew and Cade (1963). During the measurements, the mean body weight for the birds declined from 18.8 to 18.3 g. After longer periods of time in captivity, the water consumption of many birds increased to over 100 per cent of their body weight per day. However, in some cases not all the water was drunk, some being splattered about by the bird shaking its head while drinking. One bird was observed trying to bathe in the drinking tube. In another group of nine birds, four consistently "drank" over 100 per cent of their body weight

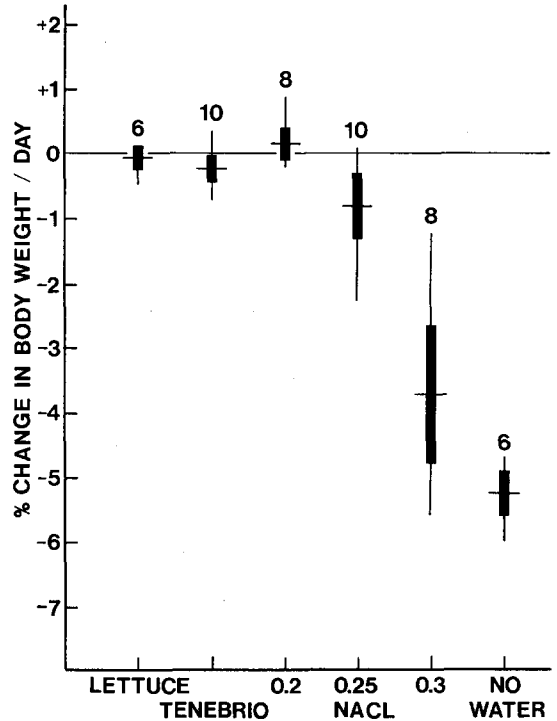


FIGURE 1. The effects of various regimes of water intake on the body weight of Sage Sparrows. Each group was provided chick-mash and either succulent food, NaCl drinking solutions, or no water, as shown. Horizontal lines indicate the mean; vertical lines, range; vertical bars, $\bar{x} \pm 2 SE$. All regimes were maintained for at least six days, except for 0.30 M NaCl, which was maintained for at least four days. Numbers indicate sample sizes.

per day while the other five drank a mean of 55.6 per cent. When this group was provided lettuce and *Tenebrio* larvae, two of the four "drinkers" reduced their drinking water intake by at least 66 and 57 per cent. The seven birds had a mean water intake of 26.3 per cent (range = 11.6-42.6 per cent).

WATER DEPRIVATION

When deprived of drinking water and provided with only a dry diet of mash, Sage Sparrows were unable to maintain their body weight, losing 5.2 per cent of their initial body weight per day (fig. 1). Four of the six birds were deprived of water until death, while the remaining birds were given water ad libitum after the eighth and ninth days of water deprivation. The mean body weight at death, or before being given water, was 57.6 per cent of the initial body weight. Assuming that the two live birds would have died within the next day (highly probably judging from their general appearance), the average length of life under conditions of water deprivation was

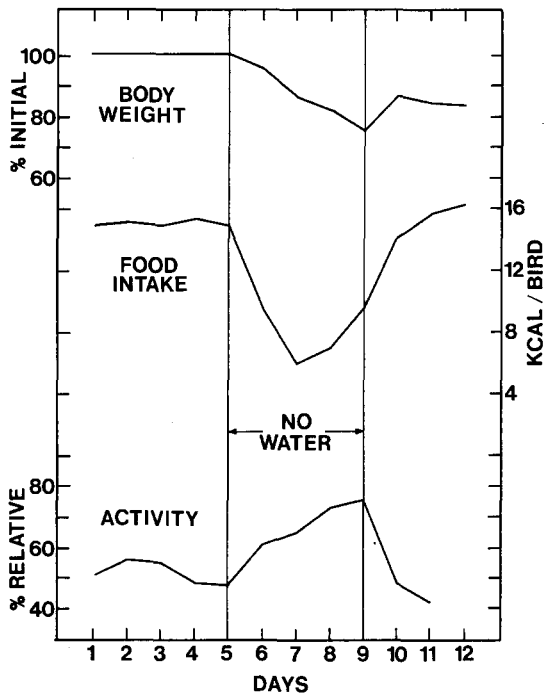


FIGURE 2. The effects of water deprivation on food intake and activity of six Sage Sparrows. Body weight is expressed as the per cent of the initial body weight; food intake as kcal/bird; activity as the ratio of total activity units to the total possible units $\times 100/\text{bird}$.

8.0 ± 0.3 days (range = 6.75 ± 0.25 – 9.6 ± 0.5 days).

The effects of water deprivation on the food intake and activity of six birds are shown in figure 2. When deprived of water, Sage Sparrows exhibited a marked reduction in food intake and an increase in motor activity. By the end of the second day of water deprivation, there was a 60 per cent reduction of gross energy intake. One bird showed a complete cessation of feeding after the first day and did not eat again until given water near the end of the fourth day of water deprivation. On the third day, all but two birds showed a slight increase in food intake compared to the previous day. On the fourth day of deprivation, five of the six birds increased their feeding to about 75 per cent of the initial intake prior to water deprivation.

Perch activity was analyzed in terms of units of activity. The 1-min graduations on the recording paper were used as units. Each unit showing any activity marks was counted, and the total was expressed as a percentage of the total possible units for the 12-hr photoperiod (720). Using this method, five of the six birds showed an increase in activity with water deprivation. However, since one unit

may contain several activity marks, the method does not allow for a true expression of the degree of increase, and consideration of the raw data shows that all birds increased their activity. Individuals exhibiting the greatest reduction in food intake showed the greatest initial increase in activity and attained the highest activity during the four days of deprivation.

UTILIZATION OF SUCCULENT FOODS

Sage Sparrows were able to maintain stable body weights when provided only with succulent foods as a water source (fig. 1) and probably are able to do so with the succulent vegetation and insects available in the habitat. With a diet of lettuce, there was a slight initial decrease in mean body weight which then stabilized and eventually returned to normal after 10 days. The results were similar but somewhat more variable for birds on a regimen of *Tenebrio* larvae. Most birds showed an initial drop in weight which then stabilized at a lower value, possibly due to the limited number of larvae provided. Although each bird was given roughly 40 larvae each day, some were lost to the bird when they were dropped or tossed out of the cage. Based on a 60 per cent water content of the total weight of the *Tenebrio* larvae eaten and including the water imbibed with the mash, the six birds maintained on this regime had a mean preformed water intake of about 2.5 ml/day.

SALT WATER UTILIZATION

The degree to which a bird can obtain usable water from saline sources depends mainly upon two factors: (1) the ability to tolerate increased levels of osmotically active particles in the blood, and (2) the concentrating capacity of the kidney. The ability of the Sage Sparrow to obtain usable water from saline sources was not exceptionally good. Birds maintained on NaCl drinking solutions of 0.25 M and above were unable to sustain normal body conditions. Body weights declined at a mean rate of 0.8 per cent of the initial body weight per day for birds on 0.25 M and 3.8 per cent for those on 0.30 M NaCl (fig. 1). Three birds on the 0.30 M NaCl regime lost 14.5 per cent of their initial weight after the first day and are not included in the results; one bird died and the other two were near death.

The effects of the various NaCl solutions on the osmotic and ionic concentrations of the blood and urine are shown in table 2. Except for blood K^+ the mean ionic and osmolar concentrations of both the blood and urine increased with the increasing molarity of the

TABLE 2. Summary of the ionic and osmotic concentrations of the blood and urine in relation to drinking solutions.

	Tap water		NaCl drinking solutions					
			0.20 M		0.25 M		0.30 M	
	$\bar{x} \pm SE$	(n)	$\bar{x} \pm SE$	(n)	$\bar{x} \pm SE$	(n)	$\bar{x} \pm SE$	(n)
Blood plasma								
No. days on regime	7		-		8		4	
Osmotic concn. (mOsmols/l)	310.0 \pm 1.1	(5)	-		314.5 \pm 3.3	(4)	362.8 \pm 2.9	(4)
Ionic concn. (mEq/l)								
Na ⁺	160.1 \pm 3.0	(5)	-		168.3 \pm 3.8	(4)	198.8 \pm 5.8	(4)
K ⁺	11.6 \pm 1.2	(5)	-		7.8 \pm 1.1	(4)	8.9 \pm 0.9	(4)
Cl ⁻	114.4 \pm 1.1	(5)	-		127.5 \pm 1.8	(4)	147.4 \pm 5.9	(4)
Urine								
No. days on regime	7		10		8		4	
Osmotic concn. (mOsmols/l)	258.0 \pm 25.3	(10)	556.0 \pm 6.6	(7)	644.1 \pm 46.6	(10)	673.8 \pm 25.2	(7)
Ionic concn. (mEq/l)								
Na ⁺	31.5 \pm 5.4	(12)	233.7 \pm 6.3	(7)	267.3 \pm 17.9	(10)	331.3 \pm 16.7	(7)
Cl ⁻	59.2 \pm 6.8	(13)	246.9 \pm 7.2	(7)	307.0 \pm 15.3	(10)	345.1 \pm 8.3	(6)

drinking solutions. However, the mean Cl⁻ and osmolar concentration of the urine showed the smallest increase. Over the range of drinking solutions, the blood Cl⁻ concentrations varied from 111 to 162 mEq/l, and osmolar concentrations varied from 306 to 371 mOsmols/l. Except with the tap water regime, the ionic and osmotic concentrations of the urine were hyperosmotic to the blood and reached a mean maximum of 345 mEq/l for Cl⁻ and 674 mOsmols/l for total solute for birds on 0.30 M NaCl. Based on the mean Cl⁻ concentrations, the maximum urine-plasma ratio for the Sage Sparrow was 2.4

Although precise fluid consumption measurements were not made for the birds maintained on the various drinking solutions, limited information indicates that fluid intake increased directly with the increase in salinity in a manner similar to that reported for the House Finch, *Carpodacus mexicanus* (Bartholomew and Cade 1958). When seven birds were transferred from tap water to 0.25 M NaCl, five exhibited a general increase in fluid consumption, whereas the other two showed a slight decrease. Similarly, when four birds were transferred from tap water through 0.1, 0.15, 0.20, and 0.30 M NaCl, there was an increase in the mean intake at 0.20 and 0.30 M.

In view of the effects of NaCl concentrations on the maintenance of body weight, ionic and osmotic regulation, and drinking, the ability of the Sage Sparrow to discriminate between various concentrations of salt solutions were tested (table 3). It appears that Sage Sparrows

are able to distinguish salt solutions of 0.15 M and greater from more dilute solutions and prefer the latter. When given a choice between tap water and 0.20 M NaCl, there was a definite preference for tap water; the birds drank almost three times as much tap water as salt solution. When tested with two salt solutions of 0.10 and 0.15 M, there was still a preference for the more dilute solution, indicating an ability to discriminate a 0.05 M difference. Group 1 drank almost twice as much, and group 2 drank four times as much of the more dilute solution. However, there was apparently little discrimination between 0.15 and 0.20 M solutions. It appears that above 0.15 M, the birds are unable to readily distinguish the 0.05 M difference.

EXCRETORY WATER LOSS

One manner by which body water loss can be reduced is through the elimination of relatively dry fecal and urinary wastes. The estimated daily excretory water losses for Sage Sparrows on various regimens of water intake and deprivation are shown in table 4. Birds maintained on ad libitum water and mash lost an estimated 4.9 g, or 27.3 per cent of their body weight per day in excretory water. The high rate of excretory water loss for this group was apparently associated with the high rate of water intake (11.0 ml/day), for when the drinking water was gradually reduced to 2.0 ml/day, the estimated daily water loss was diminished to 1.8 g, or 10.8 per cent of the body weight per day. The decrease was due to a significant

TABLE 3. Salt water discrimination of Sage Sparrows.

Test	Birds used		Days of measurement		Fluid consumption ^b		Ratio	
	Group ^a		Group		Group		Group	
	1	2	1	2	1	2	1	2
Tap water vs. 0.10 M NaCl	5	4	9	11	3.8 4.0	5.4 3.3	1.0	1.6
Tap water vs. 0.15 M NaCl	5	4	9	9	5.0 2.8	10.7 5.6	1.8	1.9
Tap water vs. 0.20 M NaCl	5	—	7	—	6.9 2.5	—	2.8	—
Tap water vs. 0.30 M NaCl	5	—	6	—	8.3 1.0	—	8.3	—
0.10 M NaCl vs. 0.15 M NaCl	5	4	12	7	6.2 3.4	11.8 2.9	1.8	4.1
0.15 M NaCl vs. 0.20 M NaCl	5	4	11	14	4.9 4.5	6.1 4.8	1.1	1.3

^a Duplicate tests.
^b ml/bird per day.

reduction both in the daily output of excrement dry weight and in the moisture content of the droppings. When the drinking water was gradually reduced, body weights declined but remained relatively stable during the administration of the restricted amount of water. The excretory water loss for birds maintained on *Tenebrio* larvae and mash with no drinking water was similar to the birds on the restricted regime (approximately 10.4 per cent of their body weight per day). The mean dry weight of the excrement and the mean per cent water content of the droppings were essentially the same for both groups. For birds deprived of water for 36 hr, the mean per cent moisture content of the fecal droppings was significantly lower than those obtained from groups provided with either restricted water or *Tenebrio* larvae, and probably represents the driest condition in which fecal droppings can normally be excreted.

GROSS AND METABOLIZABLE ENERGY INTAKE

The effects of differing regimes of water intake on the energy intake of Sage Sparrows are summarized in table 5. When the drinking water of Sage Sparrows was gradually reduced from ad libitum to 2.0 ml/day, the gross energy intake was significantly reduced from 16.44 to 12.15 kcal/bird per day, and the mean body weight declined by 1 g. However, with the decline in energy intake, the utilization coefficient (the percentage of the gross energy intake which is actually assimilated as metabolizable energy) showed an increase of 6.1 per cent, which was significant. The increase in the utilization coefficient resulted from a reduction in excretory energy output which was greater than the corresponding decrease in gross energy intake. Birds maintained on mash with only *Tenebrio* larvae as a water source had a gross energy intake which was slightly,

TABLE 4. Excretory water loss of Sage Sparrows on various regimes of water intake.

Regime	No. birds	Body wt.	Dry wt. excrement	H ₂ O, individual droppings		Estimated daily cloacal H ₂ O loss	
		\bar{x} g	\bar{x} g \pm SE ^a	$\bar{x}\%$ \pm SE	(n) ^b	\bar{x} g	% body wt.
Ad libitum water (ca. 11.0 ml/day)	6	17.8	1.5511 \pm 0.037 ^c	75.8 \pm 0.63 ^c	(81)	4.86	27.3
Restricted water (ca. 2.0 ml/day)	5	16.8	0.9615 \pm 0.037	65.5 \pm 0.56	(46)	1.82	10.8
No drinking water; <i>Tenebrio</i> larvae (ca. 2.5 ml/day)	6	17.8	0.9476 \pm 0.037	66.2 \pm 0.68	(59)	1.86	10.4
Water deprived for 36 hours	3			61.9 \pm 0.84 ^c	(20)		

^a Pooled SE—Keuls' multiple-range test.

^b Number of individual droppings analyzed.

^c Mean significantly different from others in column at 0.05 level (*t*-test).

TABLE 5. Energy intake and utilization coefficient of Sage Sparrows on various regimes of water intake.

Regime	No. birds	Body wt. \bar{x} g	Energy ^a (\bar{x} kcal/bird per day \pm SE ^b)			Utilization coefficient
			G.E.	E.E.	M.E.	
Ad libitum water (ca. 11.0 ml/day)	6	17.8	16.44 \pm 0.49	5.44 \pm 0.13 ^c	11.00 \pm 0.38 ^c	66.9
Restricted water (ca. 2.0 ml/day)	5	16.8	12.15 \pm 0.49 ^c	3.28 \pm 0.13	8.87 \pm 0.38 ^c	73.0
No drinking water; <i>Tenebrio</i> larvae (ca. 2.5 ml/day)	6	17.8	15.62 \pm 0.49 ^d	3.14 \pm 0.13	12.48 \pm 0.38 ^c	79.9

^a G.E. = Gross Energy Intake; E. E. = Excretory Energy Output; M.E. = Metabolizable Energy Intake.

^b Pooled SE—Keuls' multiple-range test.

^c Mean significantly different from other values in column at 0.05 level (*t*-test).

^d *Tenebrio* constituted 66.1 per cent of the gross energy intake; mash the remainder.

but not significantly, lower than the intake for birds on ad libitum drinking water. However, the metabolizable energy intake was significantly greater, giving a 13 per cent higher utilization coefficient. The higher metabolizable energy intake for this group was due principally to the lower excretory energy output, which was essentially the same as that for birds on the restricted regime, and possibly to the different type of food. Since there was no change in the mean body weight during the period of measurement, the higher amount of metabolizable energy available to the birds on *Tenebrio* larvae was possibly expended with higher activity. Although activity measurements were not made for these birds, birds deprived of drinking water markedly increase their activity (see Water Deprivation).

DISCUSSION

COMPARATIVE PHYSIOLOGY

Sage Sparrows apparently lack any unique physiological capabilities for maintaining water balance under conditions of water deprivation, since they steadily lost body weight and died in about eight days. The Black-throated Sparrow is the only North American desert species that can survive complete water deprivation (Smyth and Bartholomew 1966a). The House Finch (the only other closely related desert fringillid to have received intense physiological study), like the Sage Sparrow, is unable to maintain body weight when deprived of free water (Bartholomew and Cade 1956). However, Sage Sparrows lose weight at a lower rate than the House Finch and tolerate a greater weight loss. Water-deprived White-crowned Sparrows, *Zonotrichia leucophrys*, also lose body weight at a higher rate and have a slightly shorter mean survival time than the Sage Sparrow, but can tolerate a slightly greater percentage of total weight loss (MacMillen and Snelling 1966). The possibil-

ity exists that with a higher ambient relative humidity the Sage Sparrow may be able to survive longer periods of deprivation. This however, would be contrary to conditions encountered in natural situations.

Cessation of feeding with water deprivation was first suggested by MacMillen (1962) for Mourning Doves, *Zenaidura macroura*, although no food intake measurements were made to support this contention. MacMillen and Trost (1967) have suggested that in the Inca Dove, *Scardafella inca*, water deprivation results in an inability to mechanically process and digest food, which in turn results in hypothermia and a reduction in water loss. Measurements of the gross energy intake of water-deprived Sage Sparrows definitely indicated a marked reduction in food intake. A reduction in food consumption has also been reported for the Stark's Lark, Grey-backed Finch-Lark (Willoughby 1968) and the Barbary Dove, *Streptopelia risoria* (McFarland and Wright 1969). It was suggested for the latter species that the reduction in food intake with water deprivation is a water conserving mechanism, since there was a concurrent reduction in body temperature and rectal water loss. During water deprivation in the Sage Sparrow, the amount of weight lost per day by the birds was less than their estimated excretory and evaporative water losses minus the metabolic water production for watered birds. It appears, therefore, that evaporative water loss must have been reduced somewhat, since the cessation of feeding must contribute something to the total weight loss. Likewise, when transferred from ad libitum to a restricted water intake, the estimated daily excretory water loss was reduced. This reduction was due, not only to a lowering of the moisture content of the droppings, but also to a significant reduction in excrement dry weight. Because of the lower excrement dry weight, the

excretory energy output was likewise reduced, resulting in higher energy utilization coefficients. The higher utilization coefficient could be due to a longer retention of the food in the alimentary tract, possibly for the reabsorption of water, and a resulting higher assimilation of food. This was evidenced by the shorter and thicker appearance of the fecal droppings for birds on a restricted water regime. Possibly, birds in areas of limited water supply could benefit from such a response by lowering the excretory water loss and, at the same time, assimilating a higher percentage of the gross energy intake. Furthermore, with the higher percentage of available energy, less foraging time would be required, especially during the hot part of the day. The Zebra Finch showed no significant reduction in excrement dry weight with water deprivation (Calder 1964).

Reduced activity was suggested as one factor in the successful maintenance of water balance by water-deprived Savannah Sparrows, *Passerculus sandwichensis* (Poulson and Bartholomew 1962a), and Budgerygahs (Cade and Dybas 1962) because of the assumed lower rate of evaporative water loss. Therefore, the increase in activity by *Amphispiza* would at first appear to be detrimental. However, when viewed in a broader context, the increased activity could possibly be adaptive, reflecting a searching response for succulent foods. The observations that Sage Sparrows reduce their intake of mash when deprived of water, but continue to accept *Tenebrio* larvae, lends support to this view. Because of the cessation of feeding and the increase of activity in captivity, it is apparent that weight loss associated with water deprivation cannot be attributed solely to evaporative water loss, but must also involve the loss of other body components.

The ad libitum water consumption of caged Sage Sparrows is evidently much greater than needed to satisfy their normal physiological requirements. When maintained on ad libitum drinking water, fluid consumption ranged from 13 to 100 per cent of their body weight per day. However, when maintained on succulent food and no drinking water, or on a restricted drinking water regime of 2.0 ml/day, the birds were able to maintain relatively stable body weights without any impairment of health. Considering the mean values obtained for excretory water loss (ca. 1.8 g/day) and evaporative water loss (ca. 2.4 g/day) at 20°C (Moldenhauer 1969), the total daily water loss for captive Sage Sparrows maintained on *Tenebrio* larvae with a minimum free water

intake of ca. 2.6 g/day was about 4.2 g/day. The mean rate of metabolic water production was 1.30 g/day at 20°C (Moldenhauer 1969) giving a total water gain of approximately 3.9 g/day. This leaves a deficit of 0.3 g which probably can be accounted for by the difference in water vapor pressure of the evaporative water loss chamber and the cage (ca. 16 and 20 per cent relative humidity, respectively). The higher water vapor pressure would reduce the rate of water loss from the bird. From this water budget estimate, it is apparent that Sage Sparrows need a minimum of approximately 1.5–2.0 ml of free water per day to satisfy their physiological needs for water balance. This minimal water requirement was substantiated in the laboratory when several birds maintained their weight on 1.5 ml/day, but steadily lost weight when given only 1.0 ml/day.

The maximum salinity on which Sage Sparrows can maintain their body weight appears to be slightly less than 0.25 M NaCl. This concentration is maximal for a few fringillids but is lower than that for the Black-throated Sparrow and several other species (see Bartholomew and Cade 1963; Smyth and Bartholomew 1966b). It is higher than maximum levels tolerated by the Mourning Dove (Bartholomew and MacMillen 1960) and the Red Crossbill, *Loxia curvirostra*, (Dawson et al. 1965). The range of blood Cl⁻ and osmolar concentrations with ad libitum drinking of the various saline solutions are remarkably close to those of the House Finch, which has a maximum salinity tolerance of 0.25 M NaCl (Poulson and Bartholomew 1962b). The mean maximum Cl⁻ concentration of the urine for the Sage Sparrow was slightly less than that of the House Finch, but only about two-thirds that of the Black-throated Sparrow (Smyth and Bartholomew 1966a). The maximum urine osmotic concentration was lower than reported for the House Finch (Poulson and Bartholomew 1962b) but higher than that reported for the Mourning Dove (Smyth and Bartholomew 1966b). The renal capacity of the Sage Sparrow, as indicated by the urine-plasma ratio of the Cl⁻ concentrations, was the same as that of the House Finch. Both birds had a mean maximum ratio of 2.4, which was less than that for the two races of Savannah Sparrow, 3.3 and 5.5 (Poulson and Bartholomew 1962a); Budgerygah, 2.7 (Greenwald et al. 1967); and probably the Black-throated Sparrow (Smyth and Bartholomew 1966a).

A comparison of the water economies of the Sage Sparrow and the Black-throated Sparrow

indicates two differences which at least partially account for the success of the latter over the former in adjusting to conditions of water deprivation. First, while both species increase their activity with water deprivation, the Sage Sparrow markedly reduces its food intake, whereas the Black-throated Sparrow apparently does not. Secondly, the Black-throated Sparrow is more capable of concentrating its urine and producing dry excreta and thus reducing excretory water losses (depending, of course, on the daily output of excrement dry weight). Reduction in respiratory water loss may also contribute to the success of the Black-throated Sparrow, as it apparently does for the Zebra Finch, Budgerygah, and Stark's Lark (Cade et al. 1965; Greenwald et al. 1967; Willoughby 1968). Perhaps the only important difference between the Sage Sparrow and the Black-throated Sparrow is the reduction of feeding with water deprivation. How much this reduction in food intake contributes to the total daily weight loss is not known. Possibly the routes of water loss in the Sage Sparrow are sufficiently minimized to provide for a potentially favorable water balance, but because of the reduced food intake, metabolic water production and other components are diminished to create the observed weight loss. In any event, if feeding continued, the weight loss with water deprivation would be greatly diminished.

ECOLOGY

During the summer, Sage Sparrows can be observed in the sagebrush many miles from any source of surface water, and it seems unlikely that breeding birds would leave their territories for long flights to water holes. It appears that Sage Sparrows, at least during the summer months, satisfy their water demands with succulent vegetation and insects present in the habitat, as is common in several other desert birds. cursory examination of stomach contents revealed both insects and seeds, and occasionally birds were observed "fly-catching" and pecking at the vegetation.

With increasing environmental temperatures above 35°C, water losses are increased due to evaporative cooling (Moldenhauer 1969), creating an increasingly negative water balance for the Sage Sparrow. This becomes especially critical because of the low availability of water in the habitat to replenish the losses. Thus, any behavioral response by the bird to avoid heat stress would lessen the need for evaporative cooling and consequently conserve valuable body water. Such temperature-dependent behavior has been shown for

the insectivorous Cactus Wren, *Campylorhynchus brunneicapillum* (Ricklefs and Hainsworth 1968). Although no quantitative data are available, Sage Sparrows also appear to employ temperature-dependent behavioral responses. During summer days, activity was confined to the cooler morning and evening hours. The birds apparently remained inactive in the cool shaded areas of the microhabitat during the hottest part of the day. Foraging in Sage Sparrows appears to occur mainly on the ground, where they move about in the sagebrush looking for food. Here they are able to utilize the shade for protection against solar radiation. When the heat becomes extreme, they, like the Cactus Wren, perhaps shift their foraging areas to areas of thicker brush which provide a still cooler microhabitat. These facets of Sage Sparrow ecology are currently being investigated.

The water economy picture of the Sage Sparrow can be viewed as a combination of factors, consisting of several inherent physiological and behavioral preadaptations plus additional behavioral and ecological adaptations which together reduce water loss and heat stress. The several preadaptations are those already pointed out by Miller (1963). This investigation revealed no special adjustments or unusual deviations in the physiology of the Sage Sparrow to conserve body water. However, slight physiological differentials may be important from the standpoint of short-term survival as suggested by Miller (1963). The survival of the Sage Sparrow in xeric environments apparently depends mainly on adaptations which provide for the efficient utilization of succulent foods in the habitat to satisfy demands for water, and possible temperature-dependent behavioral responses to reduce heat stress. Therefore, as suggested by Ricklefs and Hainsworth (1968) for the Cactus Wren, the Sage Sparrow may be a true xerophile, not because of any unique physiological mechanisms to reduce water loss, but rather because of its behavioral responses which reduce water losses by avoidance and reduction of heat stress.

SUMMARY

This study investigated several physiological aspects of the water economy of the Sage Sparrow, *Amphispiza belli nevadensis*, as they related to its ability to inhabit xeric desert environments. When maintained in captivity on a dry diet without drinking water, Sage Sparrows gradually lost weight and died in about eight days. During the period of water deprivation, motor activity increased and gross

energy intake declined. However, Sage Sparrows were able to maintain their body weight when provided with only succulent foods as a source of water.

With ad libitum drinking of tap water, the water content of individual fecal droppings of Sage Sparrows was approximately 76 per cent. The water content was reduced to about 66 per cent for birds maintained on restricted water or *Tenebrio* larvae, and to about 62 per cent for birds deprived of water for 36 hr. The estimated daily cloacal water loss for birds maintained on mash and ad libitum drinking water was 4.9 g/day. Birds kept on restricted drinking water or *Tenebrio* larvae lost about 1.8 g/day. The reduction in daily excretory water loss was due not only to a lowering of the moisture content of the droppings but also to a reduction in excrement dry weight, which resulted in higher energy utilization coefficients for the birds on the restricted water regimes.

The renal capacity of the Sage Sparrow for concentrating electrolytes was not exceptional, with a mean maximum urine-plasma ratio of 2.4 for Cl^- . Individuals lost weight on NaCl drinking solutions of 0.25 M and above. Over a range of drinking solutions from tap water to 0.30 M NaCl, the mean blood Cl^- and osmolar concentrations ranged from 114 to 147 mEq/l and 310 to 363 mOsmols/l, respectively. The mean maximum Cl^- and osmolar concentration of the urine was 345 mEq/l and 674 mOsmols/l, respectively.

The physiological adaptations of Sage Sparrows to dehydrating conditions were not unusual for small passerine birds, and were intermediate in relation to various species of desert and non-desert birds already investigated. The successful existence of Sage Sparrows in desert environments is probably dependent upon the utilization of succulent foods to satisfy their demands for water and on temperature-dependent behavioral responses which may reduce heat stress, thereby minimizing the need for evaporative cooling.

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