

AN ABSTRACT OF THE THESIS OF

RALPH ROY MOLDENHAUER for the Ph. D.
(Name) (Degree)

in ZOOLOGY presented on January 23, 1969
(Major) (Date)

Title: THE WATER ECONOMY OF THE SAGE SPARROW,
AMPHISPIZA BELLI NEVADENSIS (RIDGWAY).

Redacted for privacy

Abstract approved: _____
Dr. John A. Wiens

This study investigated several physiological aspects of the water economy of the Sage Sparrow, Amphispiza belli nevadensis, as they relate to the ability of this species to inhabit xeric desert environments. When maintained in captivity on a dry diet without drinking water, Sage Sparrows gradually lost weight and died. 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. When birds were transferred from ad libitum drinking water to a restricted water intake of either tap water (ca 2.0 ml/day) or Tenebrio larvae (ca 2.5 ml H₂O/day), excretory water losses were diminished by about 65 percent through a reduction in both the moisture content of droppings and excrement dry weight. At the same time, there was an increase in the percentage of assimilated energy, as indicated by the utilization coefficient.

The renal capacity of the Sage Sparrow for concentrating electrolytes was not exceptional, with a mean maximum urine-plasma ratio of 2.4 for chloride. Individuals lost weight on NaCl drinking solutions of 0.25 M and above.

The thermoneutral zone of the Sage Sparrow ranged from 28 to 37°C with a standard metabolic rate of 7.24 kcal/day (mean body wt = 18.8 g; temperature = 35°C). The temperature coefficient was 5.6 percent. From 10 to 35°C the passive rate of evaporative water loss was relatively constant at ca 6.5 mg/g/hr. Above 35°C, evaporative cooling was initiated, and at high ambient temperatures and low humidities, Sage Sparrows were able to dissipate all their metabolic heat production by evaporative cooling. There was indirect evidence for a reduction in evaporative water loss with water deprivation.

The physiological adaptations of Sage Sparrows to water and heat stress 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.

The Water Economy of the Sage Sparrow,
Amphispiza belli nevadensis (Ridgway)

by

Ralph Roy Moldenhauer

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

June 1969

APPROVED:

Redacted for privacy

Assistant Professor of Zoology
in charge of major

Redacted for privacy

Chairman of Department of Zoology

Redacted for privacy

Dean of Graduate School

Date thesis is presented

January 23, 1969

Typed by Marion F. Palmateer for Ralph Roy Moldenhauer

ACKNOWLEDGMENTS

I wish to express my deepest thanks to the following people for their generous aid during this investigation: Dr. John A. Wiens, my advisor, for his encouragement and critical reading of the manuscript, and whose National Science Foundation grant (GB-6606) supported the greatest portion of the study; Dr. Robert M. Storm, Dr. Austin W. Pritchard and Dr. Ronald H. Alvarado, for their helpful suggestions and kind use of equipment; Robert W. Brocksen and the Oregon State University Oak Creek Fish Laboratory for the caloric determinations of the many food and fecal samples; my fellow graduate students, especially Stanley Anderson, Robert Parsons and Thomas Dietz, for their ideas, suggestions and untiring help; and my wife, Marlene, for her unending patience, help and encouragement.

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THE WATER ECONOMY OF THE SAGE SPARROW,
AMPHISPIZA BELLI NEVADENSIS (RIDGWAY)

INTRODUCTION

All biochemical processes necessary for life take place in an aqueous medium, and each organism must maintain the volume and solute composition of this internal medium at a relative constancy which is consistent with the life processes. Nowhere in the terrestrial environment does this homeostasis become more difficult than in the heat and aridity of deserts. With high environmental temperature, intense solar radiation and low humidities, the problem of desiccation and heat balance become acute, particularly for small animals which have high surface area to volume ratios. Yet many animals exist successfully under these conditions. For a desert vertebrate to remain in water balance all water lost in excretion and by evaporation from the skin and respiratory surfaces must be balanced by an equal amount of water intake. Likewise, to remain in thermal balance the heat gained through metabolism must be equal to the heat lost to the environment. Water demands can be satisfied from metabolic water, water in food, and drinking water, which is lacking in arid deserts except for scattered saline springs and temporary alkaline pools. The extreme heat impinging upon a desert animal can be

counteracted by avoidance (i. e., underground and shade), toleration, with an attendant increase in body temperature, or by dissipating the heat gained through active evaporation of body water, which in turn accentuates the difficulty of maintaining water balance. It is therefore apparent that the water economy of a desert species involves many interacting facets of ecology, physiology and behavior which in combination adapt the animal to this environment. Utilization of the habitat for the avoidance of heat, the efficient exploitation of the water sources, and the physiological mechanisms which reduce body water loss and heat stress all play important roles in desert existence.

As pointed out by Miller (1963) and others (Bartholomew and Cade, 1963; Cade, 1964) most birds possess several inherent physiological and behavioral preadaptations which are advantageous for existence in xeric environments. These include a high resting body temperature, the ability to tolerate a limited hyperthermia, a uricotelic kidney, high mobility and, for many birds, an insectivorous diet. With a high body temperature and an ability to tolerate hyperthermia, birds can maintain a favorable thermal gradient for the dissipation of body heat when environmental temperatures approach body temperature. The great mobility and insectivorous nature of many species allows for a more efficient utilization of the available water sources in a habitat, while uricotelism permits the removal of nitrogenous wastes with little accompanying loss of water. However,

birds also have physiological and behavioral characteristics which are disadvantageous to desert living. The diurnal and non-fossorial nature of most desert birds confines their life activities to periods when the heat and solar radiation are most extreme. In addition, in small desert birds there is a high turnover of body materials, including water, with the high metabolic rate.

The water balance of desert birds has only recently received intense study. Chew (1961), Bartholomew and Cade (1963), Cade (1964), and Schmidt-Nielsen (1964) have reviewed the early literature on avian water economy. Based on these early works Bartholomew and Cade (1963) and Cade (1964) have discussed the ecological and evolutionary aspects of avian water economy in deserts. In general, it appears that most 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 able to reduce water losses sufficiently 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) of Africa; and the Black-throated Sparrow, Amphispiza bilineata, (Symth and Bartholomew, 1966b) of North America. The physiological mechanisms by which these species reduce water loss in order to

remain in water balance are yet to be completely elucidated. However, Calder (1964, p. 408) nicely summarizes the mechanisms that could conceivably be employed to minimize water losses and thus allow a species to remain in water balance relying on oxidative water alone.

Symth and Bartholomew (1966b) showed that the Black-throated Sparrow could survive indefinitely either without water or on 0.40 M NaCl drinking solution. Measurements of urine chloride concentrations indicated levels higher than for most avian species. This sparrow inhabits some of the most extreme desert conditions in North America, breeding in sagebrush and creosote bush deserts from northeast California and southwestern Wyoming south to northern Mexico. The Sage Sparrow, Amphisiza belli, which is the only congener of the Black-throated Sparrow, also inhabits similar desert regions. 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. The breeding ranges of the two species broadly overlap in Nevada. Both species are considered granivorous and occur commonly far from surface water. Because of the similarities in distribution, habitat, and diet of these two closely-related species, a comparison of the water economy of the Sage

Sparrow with that of the Black-throated Sparrow may provide some 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

Thirty-five Sage Sparrows were used in this study. Of these, 27 were captured with Japanese mist nets during the summers of 1967 and 1968 in the vicinity of Cabin Lake Guard Station, nine miles north of Fort Rock, Lake County, Oregon, and eight were collected in a similar manner near Unionville, Humboldt County, Nevada, during November, 1966. At the time of capture, the birds were weighed to the nearest tenth of a gram 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 breeding cages (22 x 24 x 41 cm) located in a windowless room with a 12-hour photoperiod (0945-2145). Room temperatures generally remained constant at 20°C but occasionally fluctuated from 18.5 to 22°C. Although the birds remained in excellent condition on only a diet of vitamin enriched chick-starter mash,

they were occasionally given millet seed, fresh-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 tenth of a gram 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.

Water Consumption

Normal 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% 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-hour cycle plus any spillage, which was separated from the fecal droppings. Aluminum 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/gm 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 hours prior to weighing. All weighings were made to the nearest 0.05 gram 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. When depressed, the perch closed a microswitch which activated an electrical circuit to the recording pen.

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 (six and ten birds respectively) were deprived of drinking water and given lettuce (95% water) or Tenebrio larvae (60% water) along with their regular mash diet. Approximately 15 grams of freshly-chopped lettuce and about 40 Tenebrio larvae were provided the respective groups 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 effects 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 already described. 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; birds were sacrificed for blood samples the following day.

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 hour period after which a 50 to 100 microliter sample was drawn up with blood collecting tubes attached to a one ml syringe. Generally several droppings were pooled. The collecting tubes were immediately melted shut at one end and centrifuged for three to five

minutes a 5000 rpms. After a hematocrit was determined, 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 chloride determinations and a Coleman Flame Photometer was used for determinations of sodium and potassium.

Salt water discrimination tests were carried out with groups of four or five birds in a circular cage (61 cm dia x 61 cm ht) 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 water intake: ad libitum, restricted (2.0 ml/day), and no drinking water but with Tenebrio

larvae supplied (40 larvae per 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-hour collections of fecal material. Collections were made with cages fitted with metal perches, one-half inch hardware cloth floors and cork legs about 1.9 cm long. Each cage was placed on a sheet of preweighed aluminum foil so that voided fecal material would pass through the hardware cloth floor and fall on the foil. The cages and foil were located on aluminum trays to contain the dried fecal droppings and spilled food. At the end of each 24-hour 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 hours 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 Pittsburg, Pymaturing Laboratory of Ecology, 1966).

Estimates of daily cloacal water loss were made from the daily weight of the excrement and the percent water content of individual fecal droppings. Percent water content of individual droppings was determined from the wet and dry weights of freshly 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 hours at 98° C and weighed again to obtain the dry weight. In addition to the three groups of birds on differing regimes of water intake, determinations of percent moisture of individual droppings were also made for three birds deprived of water for 36 hours.

Metabolic Rate and Evaporative Water Loss

Evaporative water loss and CO₂ production were determined gravimetrically with an open flow system similar to that described by Bartholomew and Dawson (1953). The animal chamber was

constructed from a section of aluminum irrigation pipe (20 cm dia x 14.0 cm long) which was welded shut at one end with a piece of aluminum plate. An aluminum collar (22.5 outside dia x 0.6 cm thick) was welded around the open end. A plastic lid (25.3 cm dia x 0.9 cm thick) fitted with ingoing and outgoing ports was bolted to the collar and sealed with an O-ring gasket. A one-half inch hardware cloth floor was fitted 4.5 cm above the bottom of the chamber which was covered with a layer of mineral oil 1 cm deep. The oil served to trap water evaporated from any excrement that was voided during the experimental runs. Dry, CO₂-free air was introduced into the animal chamber at a rate of ca 575 ml/min. Magnesium perchlorate was used as a water absorbent and "Ascarite" as a CO₂ absorbent. Water and CO₂ given off by the bird were trapped with a series of three drying tubes and three "Ascarite" tubes, respectively. Evaporative water loss and CO₂ production were determined by the change in weight of the tubes after an experimental run of 30 minutes or one hour. Several runs of two consecutive hours were made. The tubes were weighed to the nearest 0.1 mg on a Mettler analytical balance. Prior to each run the birds were routinely fasted for 2 1/2 to 3 1/2 hours to attain a postabsorptive state. A period of about one hour was allowed for the animal to adjust to the chamber and for the system to equilibrate. All experimental runs were carried out in the dark during the daylight hours of the 24-hour cycle under a constant

temperature. Chamber temperatures were monitored with a mercury thermometer accurate to 0.1°C . The temperature for each run usually did not vary more than $\pm 0.4^{\circ}\text{C}$. Lasiewski et al. (1966) have shown that an increased flow rate at high ambient temperatures increases the efficiency of evaporative cooling by reducing the chamber humidity and increasing the difference in the water vapor pressure between the bird and the ambient air. Thus at high ambient temperatures ($43-44^{\circ}\text{C}$) the air flow through the system was increased to 1660 ml/min in order to reduce the chamber humidity. Chamber humidity was calculated from the formula presented by Lasiewski (1964). Body temperatures were taken after the high ambient temperature runs with a Schultheis rapid-registering thermometer inserted 10 mm into the cloaca immediately upon removal of the bird from the chamber. For comparison, duplicate body temperatures of six caged birds maintained at room temperature (20°C) were also taken. Birds were seized quickly and in the dark in order to minimize struggling. Temperatures were recorded within 30 sec of capture. CO_2 values for all runs were converted to volumes at STP. Heat production was calculated assuming a R.Q. of 0.70 and that 3.41 kcal are produced per g CO_2 evolved (Brody, 1945). In calculating heat loss it was assumed that 0.58 cal of heat were dissipated per mg of water evaporated.

RESULTS

Body Weight

In order to properly evaluate the water economy and bioenergetics of the Sage Sparrow, it was first necessary to establish the normal range of body weights for the species. The body weights of 77 Sage Sparrows were measured in the field shortly after collection and are summarized in 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 July 15 and October 5 and aged by plumage characteristics or degree of skull ossification. Male birds averaged slightly less than a gram more than the females for both adults and immatures, but the means are not significantly different at the .01 level of significance.

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 percent of their body weight per day, with a range of 12.7 to 99.4 percent (S. E. = 6.5). This mean value is about twice as high as that predicted from

Table 1. Summary of the field body weights of 77 Sage Sparrows (in grams).

		Adults	Immatures	Adults & Im.
	number	26	24	50
Males	$\bar{X} \pm S. E.$	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

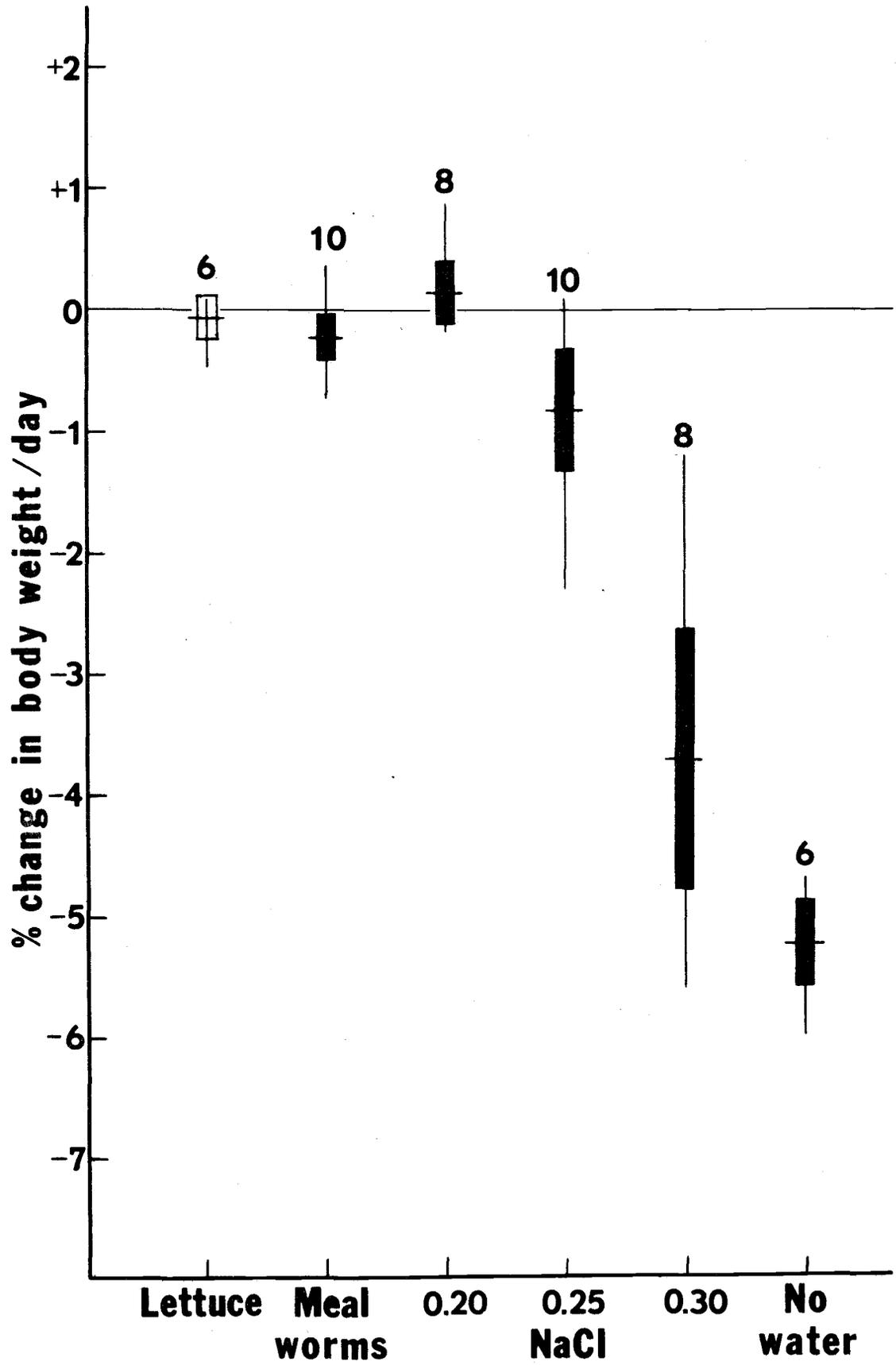
	number	7	20	27
Females	$\bar{X} \pm S. E.$	17.3 ± 0.56	17.8 ± 0.36	17.7 ± 0.30
	range	16.2 - 19.8	15.8 - 20.9	15.8 - 20.9

the water consumption curve presented by Bartholomew and Cade (1963). After longer periods of time in captivity the water consumption of many birds increased to over 100 percent per day. However, observations indicated that 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 percent of their body weight per day while the other five drank a mean of 55.6 percent. 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 percent. The seven birds had a mean water intake of 26.3 percent (range : 11.6 - 42.6 percent).

Water Deprivation

Water deprivation was used as a quick and easy method to ascertain the general physiological capabilities of the species to remain in water balance. 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 percent of their initial weight per day (Figure 1). Four of the six birds were deprived of water until death while the remaining birds were given water ad libitum after the eight and ninth days of water deprivation. The mean body weight at death, or until given water, was 57.6 percent of the initial body weight. Assuming

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, $\bar{X} \pm 2$ S. E. All birds were maintained on their particular regime for at least six days except for 0.30 M NaCl, which was for at least four days. Number indicates birds used.

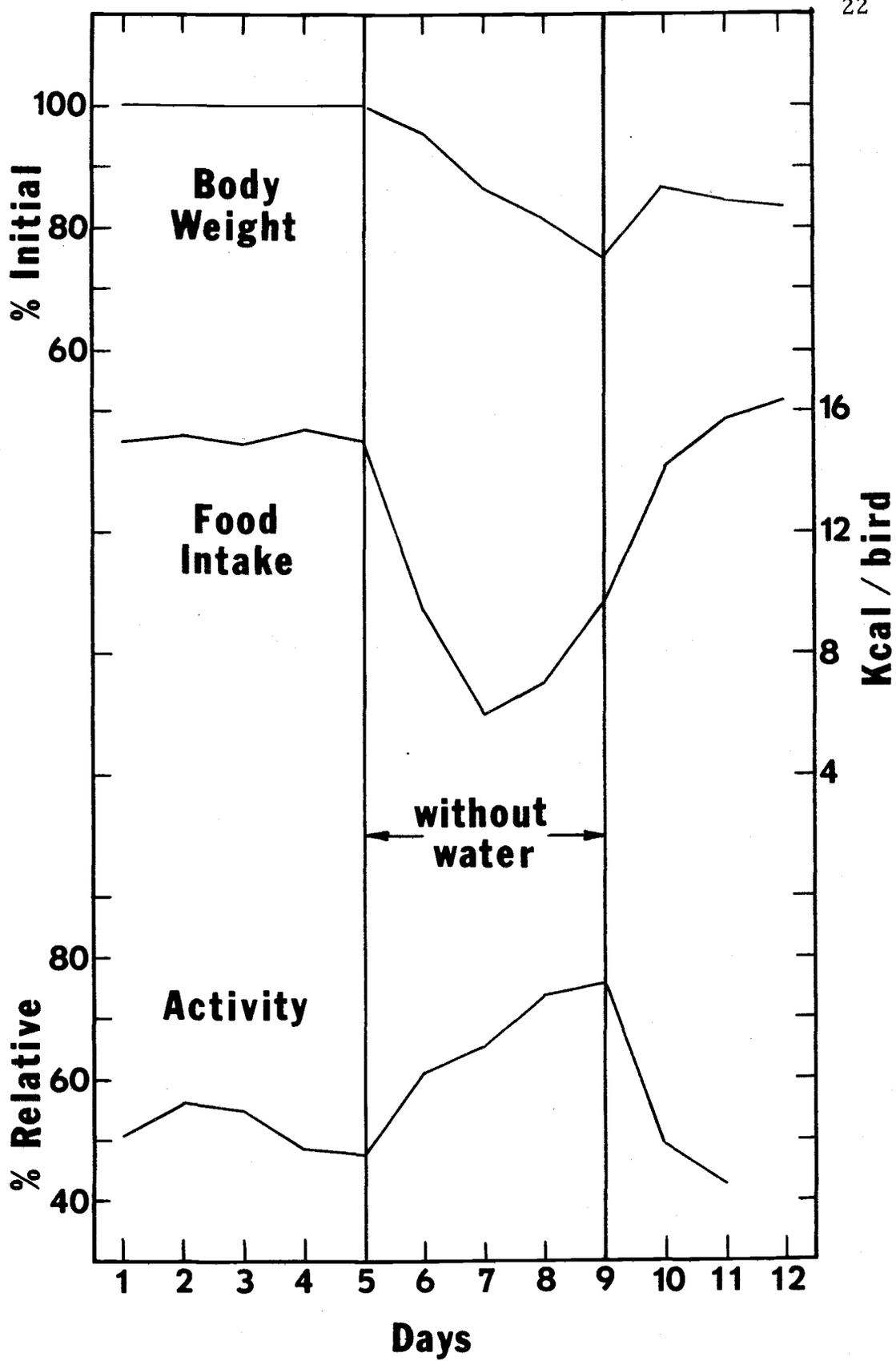


that the two live birds would have died within the next day, which was highly probable judging from their general appearance, the average length of life under conditions of water deprivation was $8.0 \pm .3$ days (range: $6.75 \pm .25$ to $9.6 \pm .5$ days).

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 exhibit 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 percent 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 percent of the initial intake prior to water deprivation.

Perch activity was analyzed in terms of units of activity. The one minute 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-hour photoperiod (720). Using this method five of the six birds showed an increase in activity with water deprivation. However, the obvious limitations of the method (one unit may contain one to several activity marks) does not allow for a true expression of the degree of increase,

Figure 2. The effects of water deprivation on food intake and activity of six Sage Sparrows. Body weight is expressed as the percent change from the initial body weight and food intake as kcal/bird; activity as the ratio of total activity units to the total possible units x 100/bird.



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 (Figure 1) and probably are able to do so with the succulent vegetation and insects available in the habitat. When given lettuce there was a slight initial decrease in mean body weight which then stabilized and eventually returned to normal after ten 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. Each bird was given roughly 40 larvae each day; however, some larvae were lost to the bird when they were dropped or tossed out of the cage. Based on a 60 percent water content of the total weight of the Tenebrio larvae eaten and including the water imbibed with the mash, six birds maintained on this regime had a mean preformed water intake of about 2.5 ml per day.

Salt Water Utilization

One aspect of the total water economy of a species is the ability to regulate the osmotic and ionic concentration of the body fluids at a relatively constant level. For animals inhabiting hot desert regions, the ability to produce a highly concentrated urine has proven to be an important physiological adaptation since it results in a conservation of body water. The concentrating ability of the Sage Sparrow 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 percent of the initial body weight per day for birds on 0.25 M and 3.8 percent for those on 0.30 M NaCl (Figure 1). Three birds on the 0.30 M NaCl regime lost 14.5 percent 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 drinking solutions. However, the mean chloride and osmolar concentrations of the blood showed the greatest increase between 0.25 and 0.30 M NaCl, whereas the mean chloride and osmolar

Table 2. Summary of the ionic and osmotic concentrations of the blood and urine in relationship to drinking solutions.

	Tap water	NaCl Drinking Solutions		
		0.20 M	0.25 M	0.30 M
<u>Blood Plasma</u>				
No. of Days on Regime	7	-	8	4
No. of Birds	5	-	4	4
Osmotic Conc. (mOsm/l) ^a	310.0 ± 1.1	-	314.5 ± 3.3	362.8 ± 2.9
Ionic Conc. (meq/l) ^a				
Na ⁺	160.1 ± 3.0	-	168.3 ± 3.8	198.8 ± 5.8
K ⁺	11.6 ± 1.2	-	7.8 ± 1.1	8.9 ± 0.9
Cl ⁻	114.4 ± 1.1	-	127.5 ± 1.8	147.4 ± 5.9
<u>Urine</u>				
No. of Days on Regime	7	10	8	4
No. of Birds	10, 12 ^b , 13 ^c	7	10	7, 6 ^c
Osmotic Conc. (mOsm/l) ^a	258.0 ± 25.3	556.0 ± 6.6	644.1 ± 46.6	673.8 ± 25.2
Ionic Conc. (meq/l) ^a				
Na ⁺	31.5 ± 5.4	233.7 ± 6.3	267.3 ± 17.9	331.3 ± 16.7
Cl ⁻	59.2 ± 6.8	246.9 ± 7.2	307.0 ± 15.3	345.1 ± 8.3
^a $\bar{X} \pm S. E.$		^b Na ⁺	^c Cl ⁻	

concentration of the urine showed the smallest increase. Over the range of drinking solutions the blood chloride concentrations varied from 111 to 162 meq/l and osmolar concentrations varied from 306 to 371 mOsm/l. Except when drinking tap water the ionic and osmotic concentrations of the urine were hyperosmotic to the blood and reached a mean maximum of 345 meq/l for chloride and 674 mOsm/l for total solute for birds on 0.30 M NaCl. Based on the mean chloride 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 one drank almost twice as much and group two 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

Another 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 grams, or 27.3 percent 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)

Table 3. Salt water discrimination of Sage Sparrows.

Test	Birds Used		Days of Measurement		Fluid Consump		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/day

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

Regime	Birds	Mean body wt (g)	Mean dry wt of excrement (g)	Mean % H ₂ O of individual droppings	Estimated daily cloacal H ₂ O loss (g)
Ad libitum water (ca. 11.0 ml/day)	6	17.8	1.5511 ± 0.0224 ^a (30) ^b	75.8 ± 0.63 ^a (81) ^c	4.86 (27.3) ^d
Restricted water (ca. 2.0 ml/day)	5	16.8	0.9615 ± 0.0234 (30)	65.5 ± 0.56 (46)	1.82 (10.8)
No drinking water; <u>Tenebrio</u> larvae (ca 2.5 ml/day)	6	17.8	0.9476 ± 0.0218 (30)	66.2 ± 0.68 (59)	1.86 (10.4)
Water deprived for 36 hours	3	-	-	61.9 ± 0.84 (20)	-

^a $\bar{X} \pm S. E.$

^bNumber of 24-hour samples

^cNumber of individual droppings analyzed.

^dPercent body weight

for when the drinking water was gradually reduced to 2.0 ml/day, the estimated daily water loss was diminished to 1.8 grams, or 10.8 percent of the body weight per day. The decrease was due to a significant reduction ($p < .01$) in both the daily output of excrement dry weight and 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, losing approximately 10.4 percent of their body weight per day. The mean dry weight of the excrement and the mean percent water content of the droppings were essentially the same for both groups and not significantly different at the .05 level of significance. For birds deprived of water for 36 hours the mean percent moisture content of the fecal droppings was significantly lower ($p < .01$) 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 gross energy intake minus the excretory energy output (urine and fecal wastes) yields the metabolizable energy which is the energy available for work, maintenance, and growth except for a

small quantity lost by the specific dynamic action of absorption (King and Farner, 1961). The percentage of the gross energy intake which is actually assimilated as metabolizable energy is the utilization coefficient. 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/day, and the mean body weight declined by one gram. However, with the decline in energy intake the utilization coefficient showed an increase of 6.1 percent which was highly significant (.001 level of significance). 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, 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 percent 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

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

Regime	Birds	Mean body wt (g)	Energy ^a			Utilization coefficient
			G. E.	E. E.	M. E.	
Ad libitum water (ca 11.0 ml/day)	6	17.8	16.44 ± 0.22 ^{bd}	5.44 ± 0.08 ^b	11.00 ± 0.18 ^b	66.9 ± 0.4 ^b
Restricted water (ca 2.0 ml/day)	5	16.8	12.15 ± 0.24	3.28 ± 0.08 ^d	8.87 ± 0.19	73.0 ± 0.5
No drinking water; <u>Tenebrio</u> larvae (ca 2.5 ml/day)	6	17.8	15.62 ± 0.35 ^{cd}	3.14 ± 0.08 ^d	12.48 ± 0.28	79.9 ± 0.3

^aG. E. = Gross Energy Intake - kcal/bird/day
^aE. E. = Excretory Energy Output - kcal/bird/day
^aM. E. = Metabolizable Energy Intake - kcal/bird/day

^b $\bar{X} \pm S. E.$

^cTenebrio constituted 66.1 percent of the gross energy intake; mash the remainder

^dMeans not significantly different at .05 level of significance

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). The higher utilization coefficient for birds on restricted water could be due to a longer retention of the food in the alimentary tract, possibly for the reabsorption of water and subsequently resulting in a higher assimilation of food. This is evidenced by the shorter and thicker appearance and the lower moisture content of the fecal droppings for birds on a restricted water regime.

Metabolic Rate and Evaporative Water Loss

Because of its major contribution to the overall loss of body water, evaporative water loss plays an important role in the total water economy of a species. Since the plumage inhibits most passive evaporation from the skin, which also lacks sweat glands, the majority of evaporative water is lost via the respiratory surfaces. This is particularly true at high ambient temperatures where evaporative cooling by panting is an essential part of thermoregulation. Metabolism, on the other hand, is important from the standpoint of both heat and water production. Heat produced through metabolism is necessary for maintenance of normal body temperatures, while the water produced as a by-product of metabolism is used in replenishing

excretory and evaporative losses. To ascertain the water relationships in Sage Sparrow thermoregulation, simultaneous measurements of CO₂ production and pulmocutaneous water loss were made over a range of ambient temperatures. The results of these measurements are illustrated in Figure 3 for metabolic rate and Figure 4 for evaporative water loss.

The thermoneutral zone of the Sage Sparrow, where the metabolic rate remained relatively independent of temperature and thermoregulation was accomplished principally by physical means, ranged from 28 to 37°C. The standard metabolic rate based on the lowest mean in the thermoneutral zone (at 35°C) was 2.43 ml CO₂/g/hr, or 7.28 kcal/24 hours, (mean body wt = 18.8 g) which is 0.3 percent higher than predicted by the Lasiewski-Dawson equation for passerines (Lasiewski and Dawson, 1967). In order to maintain thermoneutrality, the rate of heat production was progressively increased with decreasing temperatures below 28°C, the lower critical temperature. However, an eye-fitted regression line for the metabolic rate at 28°C and below extrapolates to about 50°C at zero metabolic rate, which is well above the expected normal body temperature and contrary to the Newtonian model for cooling. Apparently the shallow regression line is the result of a slight hypothermia at the lower temperatures as suggested by Greenwald, et al. (1967) for Budgerigahs. They believe that when maintained at temperatures below the

Figure 3. The effects of ambient temperature on the metabolic rate of Sage Sparrows. Numbers indicate birds used and experimental runs, respectively. ** Determinations made at high flow rate. Other symbols are as in Figure 1.

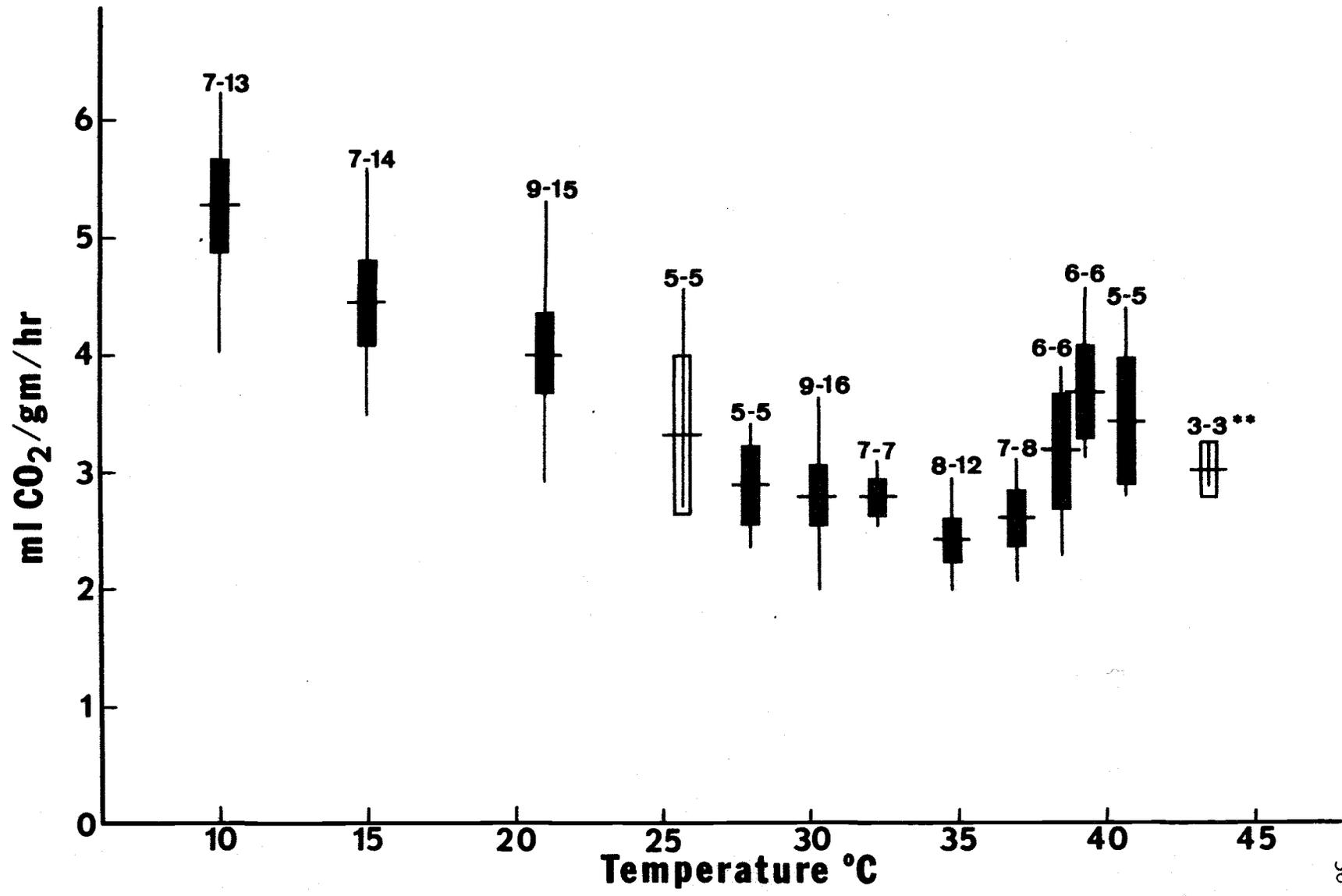
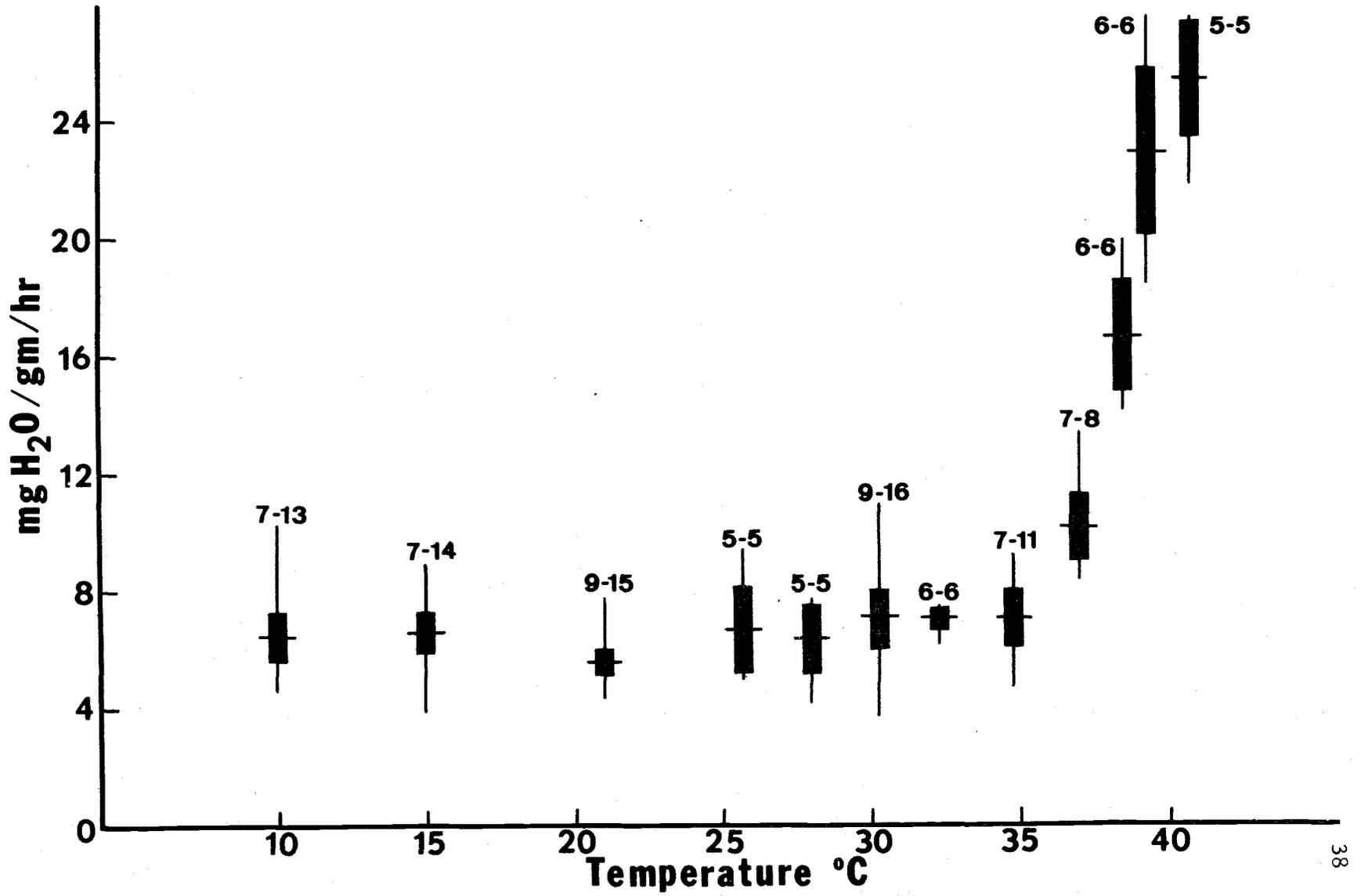


Figure 4. The effects of ambient temperature on the evaporative water loss of Sage Sparrows. See Figure 3 for explanation of symbols.



lower critical temperature, Budgerygahs adjust their body temperatures downward and consequently exhibit lower metabolic rates which result in a shallow linear regression. This regression would also result in a low temperature coefficient (the percent increase in the metabolic rate per degree centigrade below the lower critical temperature) which is an indicator of the insulating capacity of the species--the higher the temperature coefficient the poorer the insulation. The experimental Sage Sparrows possibly responded similarly to the low ambient temperatures, especially since they were kept in the constant temperature room where the metabolic rate measurements were made for periods up to a week and more. Although no body temperatures were taken at the low temperatures, the average body temperature of birds kept at 20°C was 39.2 (range: 38.0 - 41.0) which is somewhat lower than most birds of the same size in the thermoneutral zone. The temperature coefficient of the Sage Sparrow was 5.6 percent, which is intermediate to that reported for desert and non-desert birds; however, because of the probable hypofunctional condition of the birds at 10 and 15°C, the coefficient was calculated from the mean metabolic rates at 20 and 28°C.

The rate of evaporative water loss was essentially unchanged between 10 and 35°C, averaging 6.5 mg H₂O/g/hr. However, above 35°C, the upper critical temperature, there was a precipitous rise in the rate of water loss, reaching nearly a fourfold increase at

40.5° C. Nowhere in the range of ambient temperatures was the metabolic water production great enough to offset even the passive loss of evaporative water. Within the thermoneutral zone (30 to 35° C) where thermal conditions were still such that there was no need for active evaporative cooling, Sage Sparrows lost 17.1 percent of their body weight per day in evaporative water. Of this 17 percent only about 28.7 percent was replaced by metabolic means. At 10° C, where the metabolic rate was higher to meet increased thermoregulatory requirements, about 62 percent of the water loss was replaced by metabolic water production. With active evaporative cooling above 37° C the ratio of water evaporated to metabolic water production was greatly increased.

Table 6 summarizes the evaporative cooling efficiency of four Sage Sparrows determined at high ambient temperatures (near or slightly above body temperature) and low humidities. Three of the four birds were able to dissipate all their metabolic heat production by evaporative cooling for the experimental period. Bird 42 died shortly after removal from the respiratory chamber, while the other three appeared normal after removal. The poorer cooling efficiency of bird 42 can possibly be attributed to its smaller body size and the slightly higher ambient temperature of the run.

Table 6. The efficiency of evaporative cooling of four Sage Sparrows determined at high ambient temperatures and low relative humidities. ^a

Bird no.	Body wt (g)	Range of ambient temp (°C)	Body temp (°C)	EWL/HP ^b	Chamber % relative humidity ^c
502	19.2	43.8 - 43.3	41.8	1.11	24.0
2	20.7	43.7 - 43.2	42.0	1.10	25.3
46	19.2	43.9 - 43.5	42.6	1.10	26.2
42	16.0	44. - 44.0	44.6	0.83	21.3

^a All birds were tested for a period of 30 minutes.

^b EWL/HP = the ratio of the calories of heat dissipated to the calories of heat produced

^c Calculated from the equation presented by Lasiewski (1964)

DISCUSSION

Comparative Physiology

In order for a species to remain in water balance when deprived of free water, water losses through excretion and evaporation must be minimized to a point where they can be replenished by metabolic water production. The various means by which these losses can be minimized have been summarized by Calder (1964) and include such things as reduced activity, increased renal efficiency, elimination of dry excreta, thin plumage for heat dissipation, toleration of limited hyperthermia, and reduced respiratory evaporation through modification of pulmonary anatomy. Sage Sparrows apparently lack any unique physiological capabilities for maintaining water balance under conditions of water deprivation, since they steadily lose body weight and die in about eight days. Of all the North American desert species that have been investigated, only the Black-throated Sparrow, a congener of the Sage Sparrow, has such capabilities (Symth and Bartholomew, 1966b). The House Finch, which is 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 mean survival time slightly less than the Sage Sparrow but can tolerate a slightly greater percentage of total weight loss (MacMillen and Snelling, 1966).

When deprived of drinking water, Sage Sparrows reduce their feeding and, like the Black-throated Sparrow (Symth and Bartholomew, 1966b) increase their motor activity. 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. However, measurements of the gross energy intake of Sage Sparrows definitely indicated a marked reduction in food intake. Since reduced activity would result in a lower rate of evaporative water loss, it was suggested as one factor in the successful maintenance of water balance by water-deprived Savannah Sparrows, Passerculus sandwichensis, (Poulsen and Bartholomew, 1962a) and Budgeryghs (Cade and Dybas, 1962). Therefore, the increase in activity by Amphispiza at first would 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 will 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 amount of daily excretory water loss is dependent on the amount of excrement, the degree to which fecal material can be dried and still successfully voided, and the concentrating ability of the kidney. The water content of the excrement of several species is quite similar, ranging from about 80 to 60 percent depending on the regime of water intake. With ad libitum drinking of tap water, the mean water content of Sage Sparrow droppings was 76 percent, essentially the same as that reported for the Budgerygah (Cade and Dybas, 1962) but somewhat lower than that of the Zebra Finch (Calder, 1964) and the Black-throated Sparrow (Symth and Bartholomew, 1966b). When Sage Sparrows were deprived of water, the water content of droppings was reduced to about 62 percent, which was higher than the Black-throated Sparrow and about the same as the Zebra Finch and Budgerygah. Because of a higher output of excrement dry weight, the estimated daily cloacal water loss for Sage Sparrows on a restricted water intake of 2.0 to 2.5 ml/day was higher than that of the Zebra Finch on ad libitum water. The daily output of excrement dry weight is apparently dependent not only on the nature of the food and the metabolic rate of the animal but also on the water intake. When Sage Sparrows were transferred from ad

libitum to restricted amounts of water, the daily output of excrement dry weight declined significantly and the utilization coefficient increased, indicating that more food was being assimilated. 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, assimilate 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 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, and Symth and Bartholomew, 1966b). It is higher than maximum levels obtained by the Mourning Dove and the Red Crossbill, Loxia curvirostra (Dawson, et al., 1965). The range of blood chloride and osmolar concentrations with ad libitum drinking of the various saline solutions compare remarkably close to those of the House Finch, which also has a maximum salinity tolerance of 0.25 M NaCl (Poulsen and Bartholomew, 1962b). The mean maximum chloride concentration of the urine for the Sage Sparrow was 345 meg/l which was slightly less than the House Finch but is only about two-thirds that of the Black-throated Sparrow (Symth and Bartholomew, 1966a). The maximum urine osmotic concentration

was 674 mOsm/l which was lower than the 850 mOsm/l reported for the House Finch (Poulsen and Bartholomew, 1962b) but higher than that reported for the Mourning Dove (Symth and Bartholomew, 1966a). The renal capacity of the Sage Sparrow as indicated by the urine-plasma ratio of the chloride 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 (Poulsen and Bartholomew, 1962a); Budgerygah, 2.7 (Greenwald, et al., 1967); and probably the Black-throated Sparrow (Symth and Bartholomew, 1966b). The value is higher, however, than that calculated from the mean chloride values reported for the Mourning Dove drinking 0.20 M NaCl which was 1.2 (Symth and Bartholomew, 1966a).

The thermoneutral zone of the Sage Sparrow (ca 28 - ca 37°C) was slightly higher than those reported for most temperate-zone species (see King and Farner, 1961) and decidedly lower than the more specialized desert species such as the Budgerygah (Greenwald et al., 1967) and the Zebra Finch (Calder, 1964; Cade et al., 1965). High lower critical temperatures and temperature coefficients for these species are generally believed to be of adaptive value since they indicate poor insulation which allows for easier dissipation of body heat by conduction and convection. The temperature coefficient of the Sage Sparrow (5.6 percent) is intermediate to most desert and

non-desert species. The highest temperature coefficients thus far reported are ten percent for the Black-rumped Waxbill, Estrilda troglodytes, (Cade, et al., 1965), 7.9 and 8.9 percent for the Zebra Finch (Cade, et al., 1965; Calder, 1964), and 7.7 percent for the Budgerygah (Greenwald, et al., 1967).

The mean rate of evaporative water loss for the Sage Sparrow within the thermoneutral zone (30 - 35°C) was 17.1 percent of the body weight per day, or 3.14 g/day, which was slightly lower than that reported for the comparable-sized House Finch at 25°C (Bartholomew and Dawson, 1953). This value was 7.7 percent higher than predicted from the Crawford-Lasiewski (1968) equation for evaporative water loss among passerine birds. However, their formula is based on values made at varying ambient water vapor pressures which makes comparisons somewhat difficult. Sage Sparrows showed little change in the rate of evaporative water loss from 10 to 35°C; immediately above 35°C, however, active evaporative cooling was evident from the sharp rise in the rate of water loss, reaching 61.1 percent of the body weight per day at 40°C. The temperature at which evaporative cooling was initiated is comparable to the Budgerygah (Greenwald, et al., 1967) and the Inca Dove (MacMillen and Trost, 1967) but lower than the Black-rumped Waxbill and the Zebra Finch (Cade, et al., 1965). When the flow rate of the chamber was increased to produce a greater water vapor pressure

difference between the bird and the surrounding air, Sage Sparrows were capable of dissipating 110 percent of their body heat production via evaporative cooling at high ambient temperatures (43 - 44°C). Consequently, the increased cooling efficiency resulted in a lower metabolic rate preventing an explosive rise in body temperature but producing a greater negative water balance. The mean rate of water loss under the high ambient temperature-low humidity conditions was 3.9 percent of the body weight per hour which would reduce body water to a critical level in a short time. This cooling ability would, of course, be important during the hottest part of the day when temperatures approach and surpass body temperature. However, the water deficit thus created would have to be replenished with drinking water or succulent foods during the cooler mornings and evenings. An increased cooling efficiency at low ambient water vapor pressures has previously been reported by Lasiewski et al. (1966) for several species, including the House Finch, and may be true for most other birds.

The ad libitum water consumption of caged Sage Sparrows is evidently much greater than needed to satisfy its normal physiological requirements. When maintained on ad libitum drinking water, fluid consumption ranged from 13 to 100 percent 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, 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 giving a total water gain of approximately 3.9 g/day. This leaves a deficit of 0.3 grams which probably can be accounted for by the difference in water vapor pressure of the chamber (ca 16 percent R. H.) and the cage (probably greater than 20 percent R. H.). The higher the 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 to 2.0 ml of free water per day to satisfy their physiological needs for water balance. In the wild, all things being equal, this minimum quantity could be provided with approximately 37 beetles (60 percent water) about the size of adult Tenebrio monitor. Several birds maintained their weight on 1.5 ml/day but steadily lost weight when given only 1.0 ml/day.

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, although 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 than the Sage Sparrow, thus reducing excretion 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 and Budgerygah (Cade et al., 1965; Greenwald et al., 1967). 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 significantly 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. The amount of weight lost per day for water deprived birds is less than their estimated excretory and evaporative water losses minus the metabolic water production for watered birds. Therefore, it appears that evaporative water loss must be reduced somewhat, for the cessation of feeding must contribute something to the total weight loss. In any event, if feeding was continued, the weight loss with water

deprivation would be greatly diminished.

Ecology

It appears from the foregoing comparisons that the general water economy of the Sage Sparrow approaches more that of the House Finch than its generic counterpart, the Black-throated Sparrow. The Sage Sparrow, however, is somewhat intermediate. The House Finch inhabits wide areas of the arid southwest of North America but is almost always found near surface water. When deprived of water in captivity with only a dry diet, it loses body weight and dies in three or four days. However, it can maintain body weight if succulent food is available. Its apparent success in desert habitats is dependent on regular visits to surface water and succulent foods that are available (Bartholomew and Cade, 1956).

The Black-throated Sparrow, on the other hand, inhabits arid deserts far from any water, particularly during the breeding season. It is probably more independent of water than any other seed-eating species in the North American deserts. In captivity it can maintain itself indefinitely without drinking water and has the unusual capacity for processing saline water. Apparently in the wild the Black-throated Sparrow is able to satisfy its water demands with insects and succulent vegetation, visiting saline water holes only when these foods are not available, as in the fall when they feed on seeds (Symth

and Bartholomew, 1966b).

Like the Black-throated Sparrow, the Sage Sparrow also inhabits waterless tracts of desert apparently without regular visits to water holes (personal observation). However, like the House Finch, the Sage Sparrow cannot maintain its body weight on a dry diet when deprived of water in captivity. It steadily loses weight and dies in about eight days. The renal capacity of the sage Sparrow is the same as that of the House Finch and less than that of the Black-throated Sparrow. However, the ability of the Sage Sparrow to tolerate dehydration appears to be better than the House Finch.

In Oregon, Sage Sparrows arrive during the last week of March (earliest date, March 17) and remain until the middle of October (latest date, October, 22), nesting mainly from April (earliest April 5) through June (Garielson and Jewett, 1940). The latest nesting date reported by Garielson and Jewett is May 23; however, I have observed active nests during June and recorded one nest with three eggs on July 24. Full grown young birds first become common about mid-July. During the summer, Sage Sparrows can be observed in the sagebrush many miles from any sources of surface water, and it seems unlikely that breeding birds would leave their territories for long flights to water holes. At least during the summer months, it appears that Sage Sparrows 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, 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 brunneicapillus. With increasing temperatures, the Cactus Wren decreases its activity and selectively shifts its foraging location to cooler microhabitats with progressively less time being spent in the sun (Ricklefs and Hainsworth, 1968). Although no quantitative data are available, Sage Sparrows also appear to employ such 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. This response was also evident in captive birds maintained at high ambient temperatures (ca. 40°C) in a constant temperature cabinet. The birds remained quiescent with their wings held away

from the body and their feathers sleeked down to allow for greater dissipation of body heat by convection and conduction. Foraging in Sage Sparrows appears to be mainly on the ground, where they wander 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 perhaps shift their foraging areas, like the Cactus Wren, to areas of thicker brush which provide a still cooler microhabitat.

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 (1960) which include uricotelism, high body temperature, toleration of a limited hyperthermia and at least a partially insectivorous diet. This investigation revealed no special adjustments or unusual deviations in the physiology of the Sage Sparrow to conserve body water or to dissipate heat during heat stress. However, the slight physiological differentials may be important from the standpoint of short term survival, as suggested by Miller (1960) for migrants crossing desert regions. 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. This aspect of Sage Sparrow ecology, however, must await more detailed field studies.

SUMMARY

Several physiological aspects of the water economy of the Sage Sparrow, Amphispiza belli, were investigated. When deprived of water and maintained on a dry diet, Sage Sparrows lost 5.2 percent of their weight per day and died in about eight days. Concurrently with water deprivation their activity increased and the daily gross energy intake of mash declined markedly.

Ad libitum water consumption was highly variable and evidently more than normally required, since birds were able to maintain their body weight when given quantities as low as 1.5 ml/day. Also, birds kept on mash with only lettuce or Tenebrio larvae as a water source were able to maintain stable body weights.

The maximum salinity for weight maintenance in the Sage Sparrow was slightly less than 0.25 M NaCl. On the 0.25 M concentration the birds lost 0.8 percent of their body weight per day. Over a range of drinking solutions from tap water to 0.30 M NaCl, the mean blood chloride and osmolar concentrations ranged from 111 to 162 meq/l and 306 to 371 mOsm/l, respectively. The mean maximum chloride and osmolar concentration of the urine was 345 meq/l and 674 mOsm/l, respectively. The urine-plasma ratio of the chloride concentration was 2.4. Limited information indicates that fluid intake of NaCl drinking solutions increases directly with the

increase in salinity. Salinity discrimination tests also indicate that Sage Sparrows can distinguish and prefer tap water to NaCl solutions of 0.15 and above. They apparently can distinguish a 0.05 M difference in salt solutions below 0.15 M but not above.

With ad libitum drinking of tap water, the water content of individual fecal droppings of Sage Sparrows was approximately 76 percent. The water content was reduced to about 66 percent for birds maintained on restricted water or Tenebrio larvae and to about 62 percent for birds deprived of water for 36 hours. 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. Because of the lower excrement dry weight, the excretory energy output was likewise reduced, resulting in higher energy utilization coefficients for the birds on the restricted water regimes. Compared to 67 percent for birds on ad libitum drinking water, the utilization coefficient for Sage Sparrows was 73 percent for birds maintained on restricted drinking water and 80 percent for birds maintained on Tenebrio larvae as an only water source.

The thermoneutral zone of the Sage Sparrow extended from 28 to 37°C which is slightly higher than most birds. The standard

metabolic rate was 7.28 kcal/day (mean weight = 18.8 g; at 35°C). The temperature coefficient was 5.6 percent from the lower critical temperature to 21°C. Between 10 and 35°C, the rate of evaporative water loss was constant and averaged 6.5 mg H₂O/g/hr. Evaporative cooling began above 35°C, and at high ambient temperatures (ca 25 percent), Sage Sparrows were able to dissipate up to 110 percent of their metabolic heat production by evaporative cooling.

Based on water budget estimates and the rate of weight loss for water-deprived birds, there was evidence for a reduction of evaporative water loss with water deprivation.

Sage Sparrows appear not to have any unique physiological adaptations for survival in xeric environments, comparing closely in many respects to the House Finch. More than likely, Sage Sparrows satisfy their water demands with succulent vegetation and insects, and probably rely on such temperature-dependent, behavioral responses as reduced activity and avoidance to reduce water losses during periods of heat stress when they are the greatest due to evaporative cooling.

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