THE WATER ECONOMY OF THE BLACK-THROATED SPARROW AND THE ROCK WREN

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Black-throated Sparrows, *Amphispiza bilineata*, and Rock Wrens, *Salpinctes obsoletus*, are among the most conspicuous of the small birds in the desert areas of western North America and represent two quite different patterns of adaptation to heat and aridity.

Black-throated Sparrows feed largely on seeds and appear to be better adapted to desert life than any other small North American seed-eating bird. They are primarily restricted to arid regions and commonly occur far from surface water on the barren slopes of the mountains of the most extreme deserts of the continent. They breed from southwestern Wyoming and northeastern California south through Mexico to about 20° N latitude and winter from the deserts of the southern United States southward. Little information is available on aspects of their natural history other than distribution, and nothing has previously been published on their physiology. The best information on the species is that of Grinnell and Swarth (1913), Grinnell and Miller (1944), and especially Miller and Stebbins (1964).

Rock Wrens, unlike Black-throated Sparrows, are not confined to deserts and are found from British Columbia to Costa Rica. However, they are common residents throughout the deserts of western North America wherever rock piles or rocky slopes occur. Presumably they face less acute physiological problems in the desert than do Black-throated Sparrows because they are almost exclusively insectivorous (Knowlton and Harmston, 1942) and so can obtain abundant water in their food, and because they can always escape the direct sun by retreating into cracks and crevices in the rocks that they frequent (Miller and Stebbins, 1964:169).

We have combined laboratory studies of water utilization with field studies at various seasons of the year to assist in understanding the adjustments that these birds, particularly Black-throated Sparrows, have made to a singularly difficult physical environment.

METHODS

BLACK-THROATED SPARROWS

Field studies. Most of our observations were made on resident populations of *A. b. deserticola* in and near the Philip L. Boyd Desert Research Center, Riverside County, California, between March 1964 and August 1965. We also made occasional visits to Joshua Tree National Monument, the Granite Mountains near Kelso, San Bernardino County, and San Gorgonio Pass near Whitewater, Riverside County. Dawn-to-dark observations were made at a permanent water hole at an altitude of 750 meters in Carrizo Creek on the barren desert slopes of the San Jacinto Mountains where the annual precipitation is two to three inches and air temperatures above 40° C are commonplace. So that our field observations on water utilization could be based on known individuals, we captured 47 Black-throated Sparrows in mist nets as they came to drink at this water hole and then color-banded and released them. Birds were netted for laboratory studies at a water hole in the Granite Mountains or on open slopes in San Gorgonio Pass.

Maintenance. The 21 birds used were housed in a windowless room in individual cages measuring 22 × 45 × 27 cm. Lights were on from 1000 to 2200. The temperature varied between 20 and 24° C, and the relative humidity varied between 40 and 50 per cent. The birds were fed commercial-mixed bird seed, Purina chick starter, chopped lettuce, and *Tenebrio* larvae. Most of them adjusted well to cage life and remained in excellent condition. Unless otherwise specified, water with vitamin concentrate added was available at all times. In captivity the weight of the birds varied from 11 to 17 g, and the mean was about 13.5 g.

Water and NaCl solutions were provided in graduated cylinders equipped with L-shaped drinking tubes. One drinking device was used to correct for evaporation. Predetermined amounts of NaCl were administered by introducing various small quantities of NaCl solution into the stomach through a 1.5-mm O.D. polyethylene tube attached to a 1-ml syringe. The NaCl solution was colored with a dye, Fast Green FCF, so that urine which had passed through the kidneys could be differentiated from fluid which had been voided after passing directly along the digestive tract.

After administering NaCl by stomach tube, serial collections of urine were made for analysis. The birds were placed in cages with opaque sides and tops, and wire mesh floors. As excreta were produced they fell through the floors of the cages onto a roll of waxed paper that served as a conveyor belt on which the urine could be drawn from beneath the cages and picked up in a disposable pipette without disturbing the birds. The time of voiding and the color of the sample were recorded. The sample was sealed in the pipette, numbered, and frozen for later analysis. After concentrating the uric acid crystals by centrifugation, the Cl^- concentration of the supernatant fluid was measured with an Aminco-Cotlove automatic chloride titrator.

Water content of solid excreta was determined by weighing samples collected on waxed paper as described above and drying them to a constant weight at 100° C. Activity of caged birds was measured by attaching a single transverse perch to a microswitch so that each time the bird hopped onto the perch the event was recorded on an Esterline-Angus recorder and tallied on a counter in series with the recorder.

Rock Wrens

Field observations were made in the same areas as for the Black-throated Sparrows. The five birds used for laboratory studies were taken from Tujunga Wash, Los Angeles County, California. Two were captured as adults, and three were taken as nestlings and hand-reared. They were fed *Tenebrio* larvae and chopped beef heart and had water available but did not drink. They did not adjust to captivity quite as well as did the Black-throated Sparrows. Their weights when full grown ranged from 15 to 16 g. Chloride concentration of the urine was measured as described for the Black-throated Sparrows. The maximum concentration of Cl^- that could be produced in the urine was tested by administering 0.3 ml of 0.2, 0.33, and 0.5 M NaCl, stained with Fast Green, to four birds and serially collecting the urine as described for the Black-throated Sparrows.

RESULTS

Black-throated Sparrows

Field Observations

Seasonal changes in behavior. During the late fall and winter the Black-throated Sparrows formed flocks and fed on the ground on alluvial fans and rocky slopes far

TABLE 1

VISITS OF BLACK-THROATED SPARROWS TO A WATER HOLE IN CARRIZO CREEK, RIVERSIDE COUNTY, CALIFORNIA. WATCH MAINTAINED FROM DAWN TO DARK (see also fig. 1)

	Dates				
	3 Aug. 1964	14 Sept. 1964	1 Oct. 1964	7 Nov. 1964	30 July 1965
Total visits for drinking	30	72	87	143	15
Banded birds drinking	—[a]	15	12	13	2
Total visits by banded birds	—	31	24	21	2
Visits per banded bird					
Max.	—	5	3	3	1
Mean	—	2	2	1.6	1
Max. air temp. in shade, °C	33.5	32.7	31.6	22.3	31.4

[a] No birds yet banded.

from water. They often joined in loose mixed flocks with White-crowned Sparrows, *Zonotrichia leucophrys*, and Sage Sparrows, *Amphispiza belli*. By the middle of February the flocks had broken up and pair formation and singing had begun, but the birds were still independent of surface water. In 1965 there were nests with eggs by the beginning of May, and some young were out of the nest by early June. Nest location was apparently unrelated to the availability of surface water.

Use of surface water. At the permanent water hole in Carrizo Creek only a few Black-throated Sparrows began to come to drink by the end of the first week in June. During July when air temperatures often exceeded 40° C, some of the banded birds still were not drinking although they were seen within 400 meters of the water hole, and none of the young, which were out of the nest but still being fed by the parents, came to drink. As the season progressed and conditions became drier, the birds, including the young of the year, visited the water hole more and more frequently even on relatively cool days (table 1). On 15 November 1964, for instance, many sparrows came to drink although the maximum air temperature did not exceed 9° C.

On 17 November 1964 the first rain of the season fell, and by 1 December no Black-throated Sparrows were coming to drink at the Carrizo Creek water hole although it was still the only surface water in the immediate area. At this time the birds were widely dispersed over the dry slopes of the San Jacintos. As previously mentioned, they did not resume use of the water hole until the following June.

Seasonal changes in food. There is no published information on the food habits of Black-throated Sparrows other than the statement of Miller and Stebbins (1964: 255) that they eat mostly seeds but probably also eat insects and cactus fruits in summer. We have gathered information on their food by field observations and by qualitative analyses of the stomach contents of 17 birds taken at various times of year. In September and October, when the birds were drinking regularly, their food consisted exclusively of dried seeds. After the rains came and the birds were no longer drinking, their stomachs contained both seeds and fresh green plant material. Birds netted in January at San Gorgonio Pass had bills stained green, and we often saw birds near Carrizo Creek and in Whitewater Canyon eating freshly sprouted grass and other herbaceous plants. In late February insects appeared in the stomach

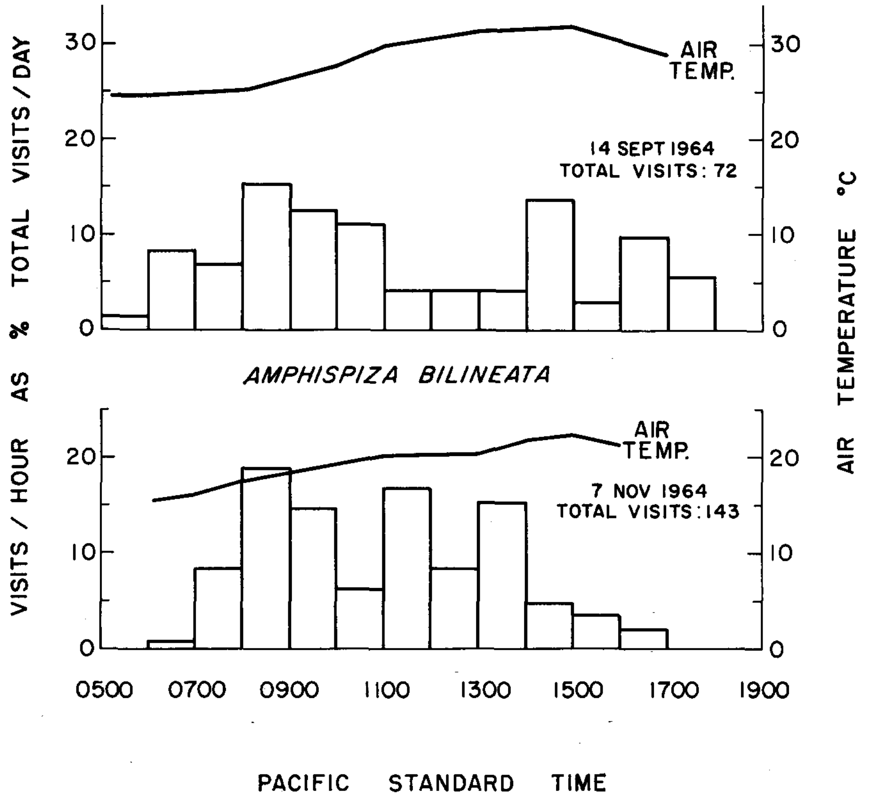

Figure 1. The drinking visits by Black-throated Sparrows to the Carrizo Creek water hole in relation to time of day and air temperature on representative days. See also table 1.

samples, and insects were the main food of both adults and nestlings throughout the spring and early summer. During this period the birds foraged in woody plants as well as on the ground, and they were sometimes seen making forays into the air to capture flying insects.

It seems reasonable to conclude that the water needs of this species are met during winter, spring, and early summer by the green vegetation and the insects which they eat. In the driest part of the year when they are eating only seeds, they drink regularly.

Black-throated Sparrows drank at the Carrizo Creek water hole during all daylight hours. On the hotter days the visits tended to be most frequent during midmorning and again in midafternoon (fig. 1). The birds not only visited water during the heat of the day, but they foraged actively during the afternoon when air temperatures were above 40° C. However, on hot days they utilized shade whenever possible and usually held their wings away from their sides. When they were active at air temperatures above 38° they often gaped their bills and panted, and interspersed their activity with repeated pauses in the shade.

Laboratory Studies

On a diet of dry seeds and chick starter and in the absence of heat stress, individually caged Black-throated Sparrows drank an average of 30.3 per cent of their

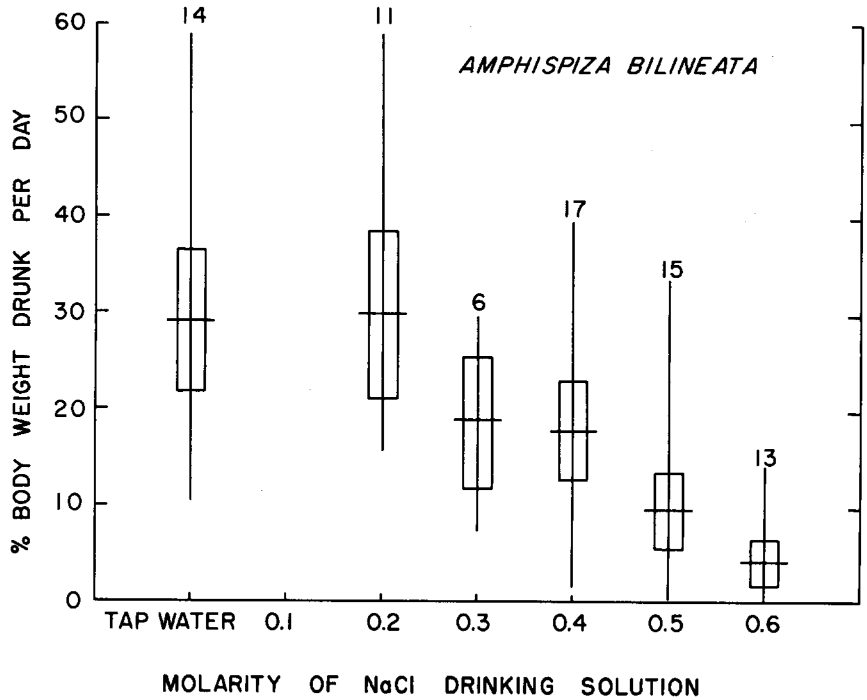

Figure 2. The relation between drinking and concentration of the drinking solution. The horizontal bar shows the mean ($\bar{X}$). The rectangle includes $\bar{X} \pm 2$ SE. The vertical line shows the range, and the numerals indicate the number of birds used. All birds measured daily for at least seven days.

body weight per day of tap water. When given 0.2 M NaCl their drinking did not change. When given more concentrated solutions, drinking decreased with increasing molarity (fig. 2). Two birds out of the 15 tested would not drink 0.5 M NaCl and five out of 13 would not drink 0.6 M NaCl. When drinking 0.4 M or less-concentrated NaCl solutions, the birds maintained their body weight. Those which drank 0.5 M and 0.6 M NaCl lost weight (fig. 3).

Unlike most small land birds, Black-throated Sparrows can survive on a dry diet without drinking. Thirteen out of 18 individuals, eating food with a free water content of 9 per cent (as determined by drying at 100° C to a constant weight), maintained their body weights after a small initial drop; several actually gained weight (fig. 4). It was not necessary to reduce the water ration gradually for birds to survive without drinking. Individual birds remained in good condition for over a month without water on a dry diet.

Activity with and without drinking water. The Savannah Sparrow, *Passerculus sandwichensis*, which is the only other small North American bird that is known to be able to live on a dry diet without drinking, manages to do so in part by reducing its activity (Poulson and Bartholomew, 1962a). This is not the case in the Black-throated Sparrow. The activity of 16 birds was measured for four days without drinking water and then for five days with water. The performances of the birds were scored in two ways; total perch-hops per 24 hours (10 birds only), and per

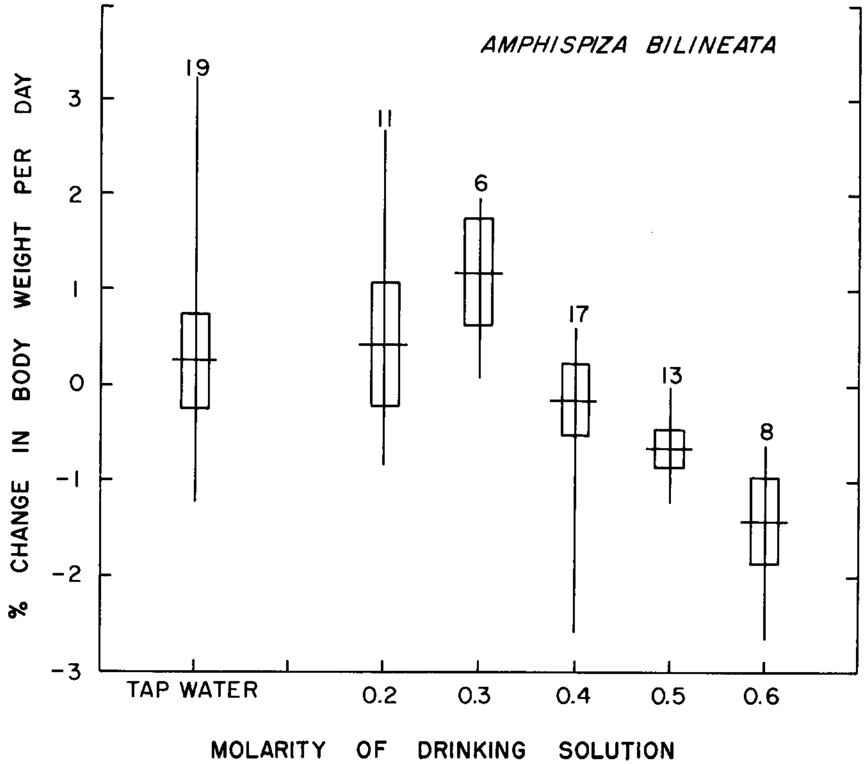

Figure 3. The relation between body weight and concentration of drinking solutions. Symbols as in figure 2. All birds were tested for seven days. Data from birds which did not drink are excluded.

cent of two-minute intervals during the hours of light in which there was perch-hopping (all 16 birds). Using total counts of perch-hops, seven out of the 10 birds measured increased activity when water was withheld. Using per cent of two-minute intervals with perch-hopping, 10 out of 16 birds increased activity when water was withheld, and two showed no significant difference. The birds that lost weight behaved no differently from those that maintained weight (fig. 5). Thus, in this species, contrary to our expectation, water deprivation in captivity did not appear to reduce activity.

Concentration of Cl^- in urine. NaCl with Fast Green dye added was given 16 times to seven birds by stomach tube, and their urine was collected serially and analyzed for Cl^-. The NaCl was given at 1000 when the lights came on, and the urine samples were collected for three to five hours. Sometimes the NaCl was immediately passed along the digestive tract, and the dye appeared in the excreta within three or four minutes. In all cases the birds produced repeated samples of un-dyed urine with an elevated Cl^- content for several hours after they had been dosed. The absence of green dye showed that the fluid had been passed through the kidneys. A typical set of records is shown in figure 6. In general the Cl^- concentration of the urine increased during the first hour, remained high for a couple of hours, and then

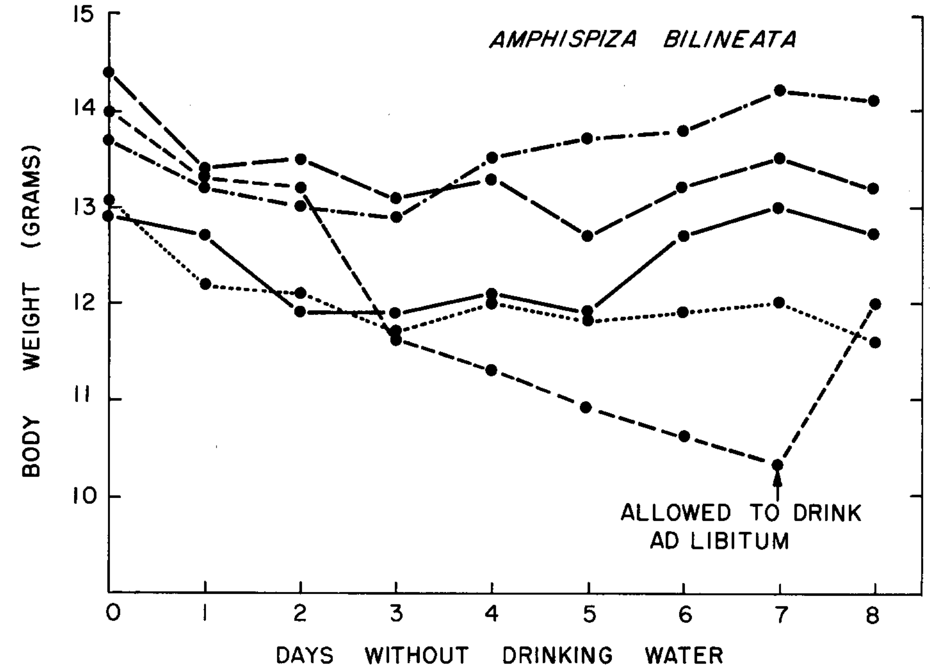

Figure 4. Body weights of birds kept on a dry diet without water. In each case day zero is the third day after capture. Only five of the 18 birds tested are shown. These records are typical.

declined to the normal levels of less than 50 mEq/liter. All of the birds produced urine with a Cl^- concentration greater than 350 mEq/liter. Concentrations above 500 were common, and one bird produced urine with 703 mEq Cl^-/liter.

Water content of excreta. Birds on a diet of seed and chick starter with water available produced relatively moist excreta; the mean water content of 25 samples of nonliquid excreta was 81 ± 6.6 per cent (range 67 to 91). When water was withheld for a week the excreta became drier; the mean water content of 17 samples of nonliquid excreta was 57 ± 12.7 per cent (range 31 to 80).

Rock Wrens

Field observations. Rock wrens were resident at Carrizo Creek in the vicinity of the permanent water hole where our all-day watches were made. We never saw them drink even though they sometimes foraged within 10 meters of the water.

Concentration of Cl^- in the urine. The Cl^- concentration in the urine of wrens on a diet of meal worms and beef heart varied between 50 and 167 mEq/liter. The maximum concentrations of urinary Cl^- increased with increasing dosage of NaCl (fig. 7), and the maxima from each of the four birds tested were 325, 373, 387, and 403 mEq/liter. In each experiment the peak concentration was reached within an hour and declined steadily thereafter.

DISCUSSION

In the laboratory most Black-throated Sparrows can get along without water even on a dry diet. From this, we infer that the species requires unusually little

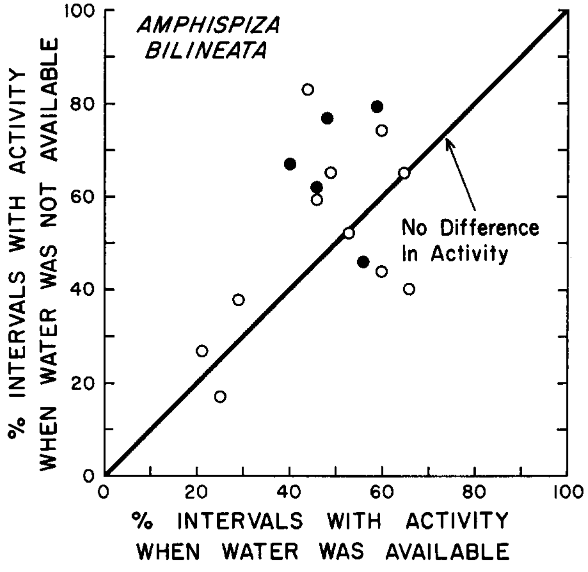

Figure 5. The effects of water availability on the activity of Black-throated Sparrows maintained on a dry diet of mixed bird seed and chick starter. The points show the per cent of two-minute intervals during the light period in which a given bird hopped on its perch. The unshaded circles are for birds that maintained body weight. The shaded circles are for birds that lost weight.

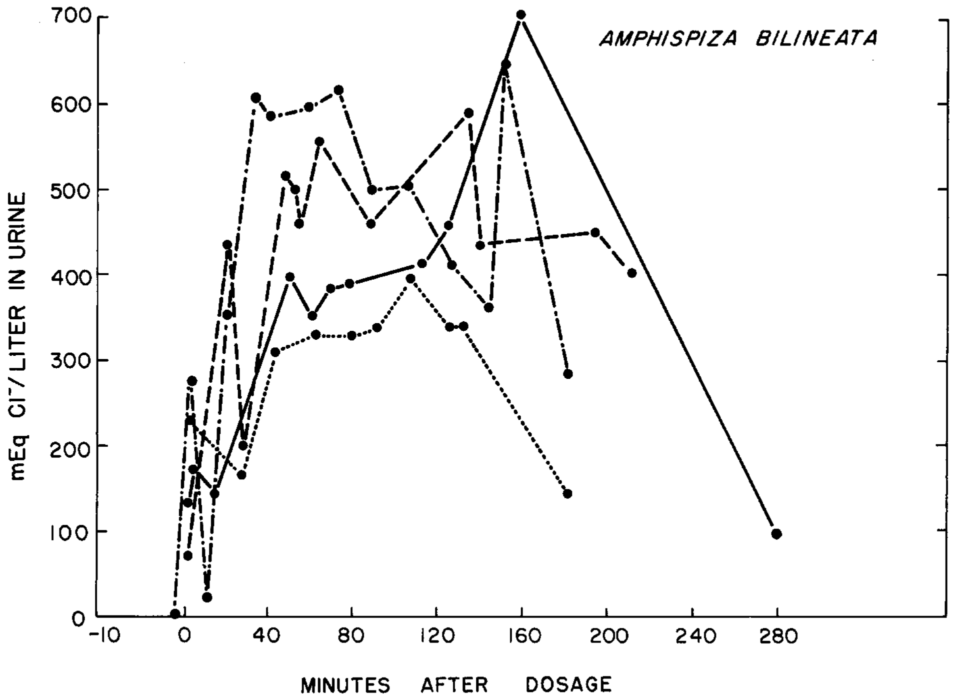

Figure 6. Concentrations of chloride in successive samples of the urine from four Black-throated Sparrows given 0.3 ml of 0.5 M NaCl by stomach tube. NaCl administered at time zero.

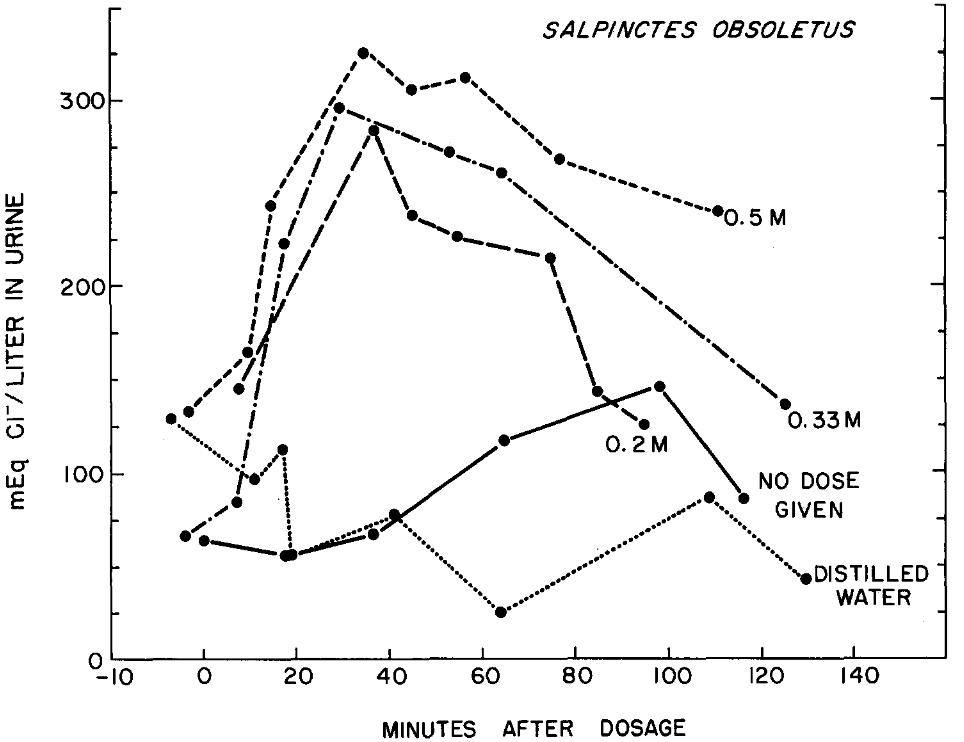

Figure 7. Concentrations of chloride in successive samples of urine from one of the four Rock Wrens given 0.3 ml of various NaCl solutions by stomach tube on different days. The NaCl was given at time zero.

water. Whenever climatic conditions are such that these sparrows can find green vegetation or insects, they do not need to drink even if air temperatures are high and solar radiation is intense. Consequently some individuals can be found, even in midsummer, many miles from water. They do, however, avoid the hot sinks and low valleys and confine their activities to the relatively cooler slopes and higher basins. At those times when Black-throated Sparrows feed primarily on seeds, they utilize extra water and drink regularly. Their dependence on drinking during the dryest part of the year is shown by the fact that within two weeks of the first rains they left the vicinity of the water hole and no longer drank there even though it was still the only surface water in the study area.

We did not survey the insect fauna of the Deep Canyon area, but Evert Schlinger of the University of California, Riverside, was taking weekly samples of the insects there throughout the period of our study. He tells us that day-flying insects were common only from March through June and were scarce from July through February. Thus, the time at which the Black-throated Sparrows began to visit the water hole corresponded closely with the time at which day-flying insects began to become scarce. The time at which the birds stopped visiting the water hole corresponded with the first appearance of new green vegetation.

The capacity of the Black-throated Sparrow to survive in the laboratory on a dry seed diet without drinking is as great as that of the Zebra Finch, *Taeniopygia castanotis*, which lives in the Australian deserts (Calder, 1964; Cade *et al.*, 1965). In this respect the Black-throated Sparrow excels all other seed-eating species of North America for which data are available (see Bartholomew and Cade, 1963), except for a few individual Savannah Sparrows from salt-marsh areas (Poulson and Bartholomew, 1962a).

If one uses the capacity to obtain water from NaCl solutions and the capacity to concentrate Cl^- in the urine as indexes of the ability to conserve water, the performance of the Black-throated Sparrow is unusually good. It has twice the capacities of the House Finch, *Carpodacus mexicanus* (Poulson and Bartholomew, 1962b), and the Mourning Dove, *Zenaidura macroura* (Smyth and Bartholomew, in press), both of which occupy the desert but are dependent on drinking throughout the year. Black-throated Sparrows, however, are less able to process NaCl than are salt-marsh Savannah Sparrows (Poulson and Bartholomew, 1962a).

Reduction in pulmonary water loss should also facilitate survival on reduced water rations. One way of reducing pulmonary water loss is to be inactive. The Savannah Sparrow (Poulson and Bartholomew, 1962a), the House Finch (Poulson and Bartholomew, 1962b), and probably the Budgerygah, *Melopsittacus undulatus* (Cade and Dybas, 1962), reduce their voluntary locomotor activity when given dry food but no water; the Black-throated Sparrow does not.

The water content of the excreta of Black-throated Sparrows with drinking water available was 81 per cent, which is indistinguishable from that of Zebra Finches (Calder, 1964) and Budgerygahs (Cade and Dybas, 1962) under similar conditions. When water was withheld the water content of the excreta of this sparrow fell to 57 per cent, which is slightly, but probably not significantly, lower than that of these two other species.

It is not necessary to invoke evolution of special physiological adjustments in water economy to explain the success of Rock Wrens in the desert. They forage for insects by digging and probing and also commonly eat ants and thus are not dependent on day-flying insects which are only seasonally available. Their diet, therefore, supplies them with water throughout the year. Moreover, they can usually escape the heat by retreating deep into crevices in the rocks where they live. Wauer (1964) suggests that in Death Valley they may withdraw to higher elevations during the hottest months of the year. In the one facet of their physiology which we examined, their ability to concentrate Cl^- in their urine, they were more effective than the House Finch and the Mourning Dove, but much less effective than the Black-throated Sparrow.

It is our interpretation that the Rock Wren's success in the desert is a product of its general mode of life and is not dependent on special physiological adaptations. However, the Black-throated Sparrow presents a more interesting case. In North America it is probably the best adjusted to the desert of any seed eater. Its pattern of seasonal shifts in water source and its ability to concentrate its urine and dry its feces may approach the evolutionary limit that a small seed-eating passerine can attain, and certainly it can serve as a model with which the patterns of adaptation of the finches of the more ancient deserts of Asia, Africa, and probably Australia can profitably be compared.

SUMMARY

In southern California, Black-throated Sparrows do not need to drink when they

can eat green vegetation or insects, but in areas where water is available they drink regularly when they are mainly eating seeds. Rock Wrens do not need to drink but obtain water from the insects they eat.

On a dry diet in the laboratory Black-throated Sparrows drank 30 per cent of their body weight per day when given water *ad libitum*, but most individuals survived indefinitely without drinking. When deprived of water, they did not reduce their activity. Drinking of NaCl solutions decreased with increasing molarity. Birds maintained their body weight when drinking 0.4 M or less concentrated solutions of NaCl. Birds which drank 0.5 M or 0.6 M NaCl lost weight.

When given NaCl by stomach tube, Black-throated Sparrows commonly produced urine with a Cl^- concentration of more than 500 mEq/liter, and one bird produced urine with 703 mEq/liter.

When drinking water was withheld, the water content of the excreta of Black-throated Sparrows, which is normally about 81 per cent, decreased to 57 per cent.

The maximum urinary chloride of Rock Wrens given NaCl by stomach tube varied from 325 to 403 mEq/liter.

The insectivorous habits and habitat preferences of Rock Wrens apparently allow them to avoid the heat and aridity of the desert without making any special physiological adjustments in their water economy.

Black-throated Sparrows are more independent of drinking water than other small seed-eating North American birds for which there are data, and they have unusual capacity for processing saline water and concentrating electrolytes in their urine.

ACKNOWLEDGMENTS

We are indebted to Lloyd Tevis of the Philip L. Boyd Desert Research Center for help in establishing our field program and to Harry Coulombe for effective help in the field and the laboratory.

This research was supported by a grant from the National Science Foundation, GB-966.

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17 August 1965.