ENERGY INTAKE BY HYDROPENIC CHIPPING SPARROWS (*SPIZELLA PASSERINA PASSERINA*) MAINTAINED ON DIFFERENT DIETS

RALPH R. MOLDENHAUER
AND
PATRICIA G. TAYLOR

Department of Biology
Sam Houston State University
Huntsville, Texas 77340

INTRODUCTION

Water deprivation tests have been used to study the physiological capabilities of small desert birds to remain in water balance when maintained solely on a dry diet of seeds. In order to survive such conditions, a bird must employ certain physiological and behavioral adjustments so that water loss through evaporation and excretion is minimized to a point where it can be balanced by metabolic water and water ingested with the food. In addition, the seeds must be mechanically processed and assimilated to satisfy energy requirements, even though water is not readily available. Several species are capable of maintaining water and energy balance for prolonged periods without free water (Smyth and Bartholomew 1966; Ohmart and Smith 1971). However, little work has been done on the effects of water restriction and deprivation on avian energy balance. In some birds, gross energy intake and excretory energy output are altered during water deprivation and restriction (Willoughby 1968; McFarland and Wright 1969; Moldenhauer and Wiens 1970), but little is known about the ecological implications and relationship of these two values before and after deprivation. Furthermore, comparisons have been hindered by the diversity of the diets utilized in water economy studies. These diets include mixed bird seed (Bartholomew and Cade 1956), commercial millet (Willoughby 1968), chick starter mash (MacMillen and Snelling 1966; Moldenhauer and Wiens 1970; Anderson 1970), or combinations of these (Poulson and Bartholomew 1962; Ohmart and Smith 1971), all of which differ in texture, protein and salt content, and calorific value. Perhaps these different diets affect the outcome of water economy studies, resulting in data which may not be truly comparable. This study provides information on the effects of water restriction, water deprivation, and diet on the energy balance of the eastern Chipping Sparrow (*Spizella passerina passerina*).

MATERIALS AND METHODS

The 32 Chipping Sparrows used in this study were captured with baited traps in the vicinity of Huntsville, Walker County, Texas, between January and March 1971. Shortly after capture, the birds were weighed with a triple beam balance to the nearest 0.1 g and transferred to Sam Houston State University, where they were maintained in large holding cages (45 × 56 × 68 cm) on a diet of Purina chick starter mash and water.

Experiments were carried out in a windowless room with a 12-hr photoperiod (09:00–21:00). Room temperatures remained relatively constant at 26°C, with occasional fluctuations from 23 to 28°C. The relative humidity was not controlled and averaged about 55% (range 30–71).

Experimental birds were housed individually in small cages (24 × 41 × 42 cm), equipped with glass feeders, one-half inch hardware cloth floors, and wooden legs which elevated each cage about 1 cm. Each cage was placed inside a wax-lined cardboard box (42 × 10 × 57 cm) to contain any spilled food. A piece of preweighed aluminum foil was placed beneath each cage to collect the fecal material as it fell through the hardware cloth floor.

Measurements of ad libitum tap water consumption were made with inverted 15 ml graduated cylinders fitted with L-shaped drinking tubes (Bartholomew and Dawson 1954). For birds restricted to a regimen of 4 ml or 2 ml of tap water, similar L-shaped drinking devices, without graduated cylinders, were filled by syringe with the appropriate amount of water. One control drinking device was used to measure evaporation during any regimen.

Estimates of metabolizable energy intake were made under four regimens of fresh water intake: ad libitum, restricted to 4.0 and 2.0 ml/day and no drinking water. Each experimental group was initially placed on a diet of chick starter mash (ca. 8.2% water) or "millet" seed (actual: 75% millet and 25% canary seed; ca. 9.2% water) with ad libitum tap water for a 3-day period. At the end of this time, ad libitum water consumption was terminated. Then half of the group was placed on 4 ml/day of tap water while the other half received 2 ml/day for an additional 3-day period. The entire group was then given ad libitum water for several days before being deprived of free water until death. Other groups of hydrated birds were immediately water-deprived, omitting the restricted regimens. One group of five birds was placed on a mixed diet of mash and millet. These birds received ad libitum water for 3 days before being deprived of water.

Food consumption and excretory output were de-

The Condor 75:439–445, 1973

TABLE 1. The mean body weights and ad libitum water consumption of Chipping Sparrows on different diets.

Diet	No. birds	Body wt. $\bar{x}$ g ± SE	Water consumption % body wt/bird/day ± SE
Mash	20	12.5 ± 0.2	46.2 ± 3.8
Millet	11	11.8 ± 0.4	24.6 ± 2.5
Mixed	5	12.1 ± 0.5	28.1 ± 3.7

termined for each 24-hr period. Prior to the beginning of the daily photoperiod, the food for each bird was weighed to the nearest 0.01 g. The container of food and a clean hardware cloth floor were then placed in each cage along with the specific water regimen. The cage was then set inside a clean cardboard box containing aluminum foil that had been preweighed to the nearest 0.01 mg. Each bird was weighed at this time to the nearest 0.1 g. A sample of food which had been equilibrated to room humidity conditions was weighed and dried at 90°C for 24 hr to determine moisture content.

At the end of each 24-hr period, the cardboard box, aluminum foil, hardware cloth floor, and food container were removed and replaced. Any food spilled during the period was separated from the fecal material on the aluminum foil or in the cardboard box and replaced into the food container. The fecal material adhering to the hardware cloth floor was scraped free and combined with the loose fecal droppings separated from the food. The gathered fecal droppings and aluminum foil which contained adhered fecal material were dried at 90°C for 24 hr along with the residual food. After drying, the food, aluminum foil, and gathered fecal droppings were again weighed to the nearest 0.01 mg. For those birds surviving water deprivation for 21 days, estimates of energy intake were made on days 10, 16, and 21, in addition to the first 3 days following water deprivation.

Caloric determinations of the food and fecal material were made with a Parr Instrument Company oxygen bomb calorimeter. The mean caloric values of 10 samples of mash and 10 samples of millet were 4.2806 (SE = ±0.0198) and 4.3810 (SE = ±0.2987) Kcal/gm dry weight, respectively. Metabolizable energy was taken as the gross energy intake minus

TABLE 2. Summary of weight changes of Chipping Sparrows on various regimes of water intake for 3-day period.

Water regime	No. birds	% initial body wt.[b]	Rate wt. loss %/bird/day[b]
4.0 ml[a]			
Mash	8	94.5 ± 1.0	1.9 ± 0.3
2.0 ml			
Mash	9	87.5 ± 0.8	4.9 ± 0.3
Millet	7	100	
No drinking water			
Mash	11	68.2 ± 1.9	10.6 ± 0.4
Millet	13	78.6 ± 3.2	7.2 ± 0.4
Mixed	5	71.0 ± 2.0	9.7 ± 0.8

[a] Birds placed on millet and 4.0 ml of water maintained their body weight, but did not consume all of the water.
[b] $\bar{x}$ ± SE.

the excretory output (King 1961). Except for the single 24-hr determinations for birds surviving prolonged water deprivation, excretory energy was determined for each bird from caloric measurements of three consecutively pooled 24-hr collections of fecal material.

RESULTS

BODY WEIGHT AND WATER CONSUMPTION

The mean body weight for all birds, regardless of diet, was 12.2 (SE = ±0.33) g. Although body weight was not altered appreciably by any diet, ad libitum water consumption was significantly higher for birds eating mash than for those eating millet or a mixed diet (table 1).

WEIGHT CHANGES DURING WATER RESTRICTION AND DEPRIVATION

The changes in body weight during the 3-day period of water restriction and deprivation are summarized in table 2. While birds on a diet of mash and 4 ml of drinking water lost 1.9% of their initial body weight per day, birds on the millet diet and the same water regimen maintained a constant body weight even though all of the available water was not consumed. Birds restricted to 2 ml of water and mash lost weight at a rate of 4.9% of their initial body weight per day; however, there was no change in body weight for birds maintained on millet and 2 ml of water. With no water, mash-fed birds had the highest rate of weight loss.

Figure 1 illustrates the effect of prolonged water deprivation on the body weight of birds on the three different diets. Nine Chipping Sparrows maintained on millet seed initially lost 6.5% of their body weight per day. However, four of the nine birds stabilized their body weight and after 21 days their mean weight was 78.4% of their initial body weight. At the end of 21 days, two of the birds were given water, whereas the other two birds lived until day 22 and 31 of water deprivation. The mean number of days of survival for the other five millet-fed birds was 6.8 days (range 4–11). None of the birds on the mash or mixed diet lived beyond the seventh day of water deprivation. Mash-fed birds lost 10.1% of their body weight per day and had a mean weight at death of 62.2%. The mean number of days of survival without water was 3.4 days (range 2–5). Chipping Sparrows on the mixed diet lost 9.7% of their initial body weight per day, and mean weight at death was 57.0% of the initial body weight. The mean length of survival without water was 5.8 days (range 5–7).

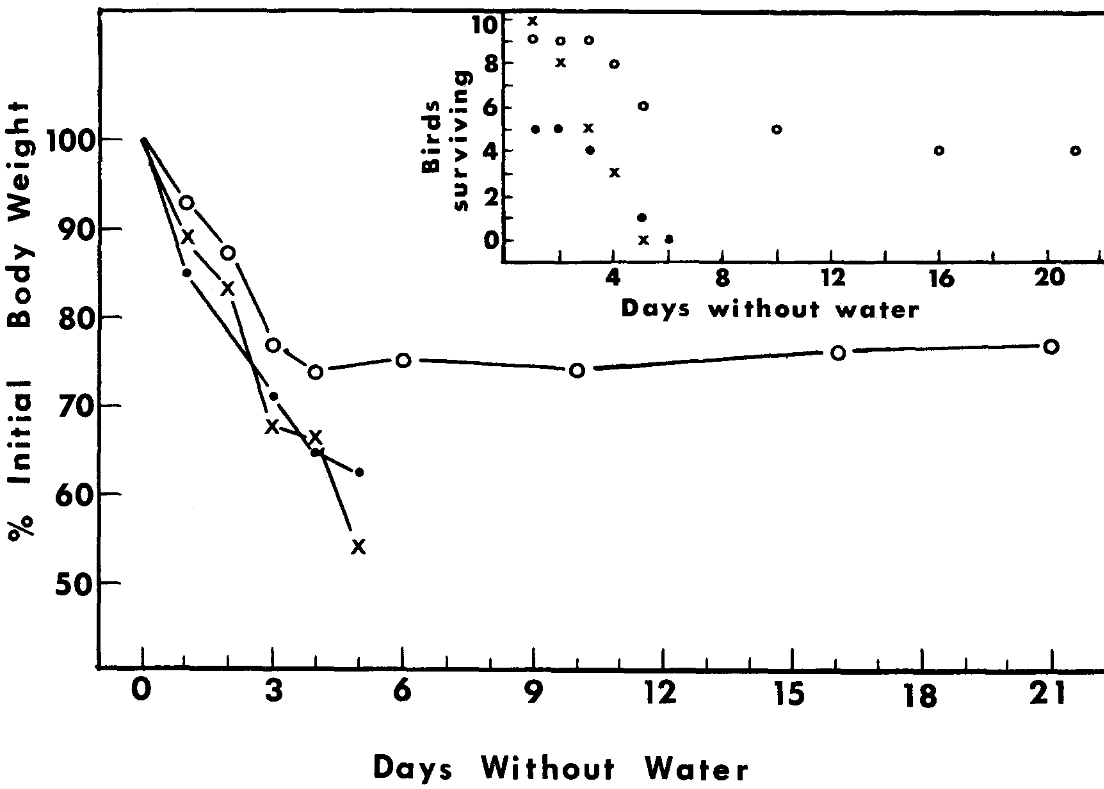

FIGURE 1. The effects of water deprivation on the mean body weight of Chipping Sparrows maintained on mash (X), millet (○) and mixed (●) diets.

INITIAL EFFECTS OF WATER RESTRICTION AND DEPRIVATION ON ENERGY INTAKE

Regardless of the diet, gross energy intake, excretory energy output, and metabolizable energy decreased initially as the amount of drinking water was reduced (table 3). The utilization coefficient for birds on the mash diet remained fairly constant (ca. 69%) on ad libitum, 4 ml, or 2 ml of drinking water. However, birds receiving mash and no drinking water had a utilization coefficient of 63.9%. The coefficient for millet-fed birds was higher (> 80%) and increased slightly as the drinking water was reduced.

TABLE 3. Mean energy values of Chipping Sparrows on mash and millet diets with various water regimes for 3-day period.

Water regime	No. birds	Body wt. $\bar{x}$ g	Energy[a] ($\bar{x}$ Kcal/bird/day ± SE)			Utilization Coefficient
			G.E.	E.E.	M.E.	
Ad libitum						
Mash (5.8 ml/day)	20	12.5	12.50 ± 0.40[c]	3.84 ± 0.14[c]	8.66 ± 0.27[c]	69.3 ± 0.3[c]
Millet (2.9 ml/day)	11	11.8	9.28 ± 0.58	1.69 ± 0.25	7.59 ± 0.45	81.8 ± 2.1
Restricted (4.0 ml/day)						
Mash	8	12.0	10.03 ± 0.35	3.05 ± 0.11	6.98 ± 0.28	69.6 ± 0.9
Restricted (2.0 ml/day)						
Mash	9	10.6	7.23 ± 0.31	2.15 ± 0.09[c]	5.08 ± 0.23[c]	70.3 ± 0.4[c]
Millet	7	11.7	8.75 ± 0.72	1.36 ± 0.24	7.39 ± 0.53	84.5 ± 1.7
No drinking water						
Mash	13	8.7	1.85 ± 0.31[c]	0.73 ± 0.07	1.12 ± 0.26	63.9 ± 3.6[b, c]
Millet	13	9.2	4.12 ± 0.61	0.62 ± 0.10	3.50 ± 0.51	85.2 ± 0.7[b]

[a] G.E. = Gross Energy Intake; E.E. = Excretory Energy Output; M.E. = Metabolizable Energy.
[b] Calculated only for those birds that consumed food on all 3 days.
[c] Significant difference between means of mash and millet diets within a particular regime ($\alpha = 0.05$).

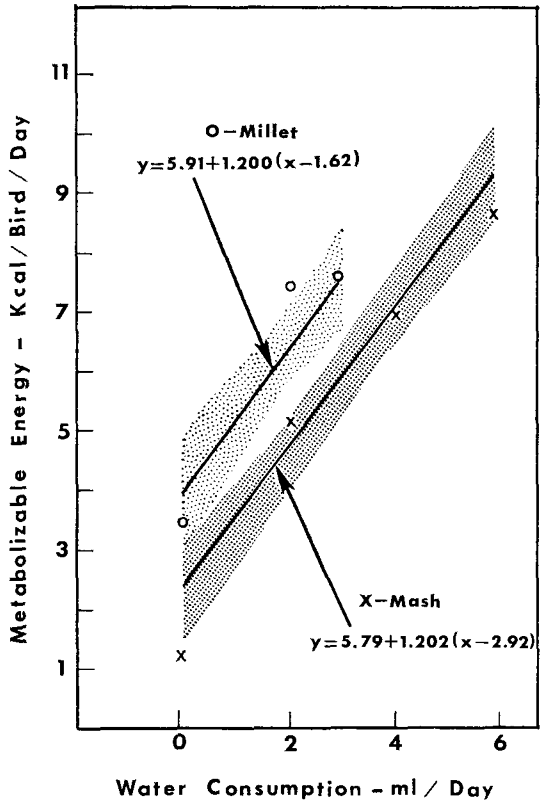

FIGURE 2. The relationship between water intake and metabolizable energy intake of Chipping Sparrows on mash (X) and millet (O) diets. Solid lines indicate regression lines for designated diet. Stippled areas include 95% confidence limits. Sample size indicated in table 3.

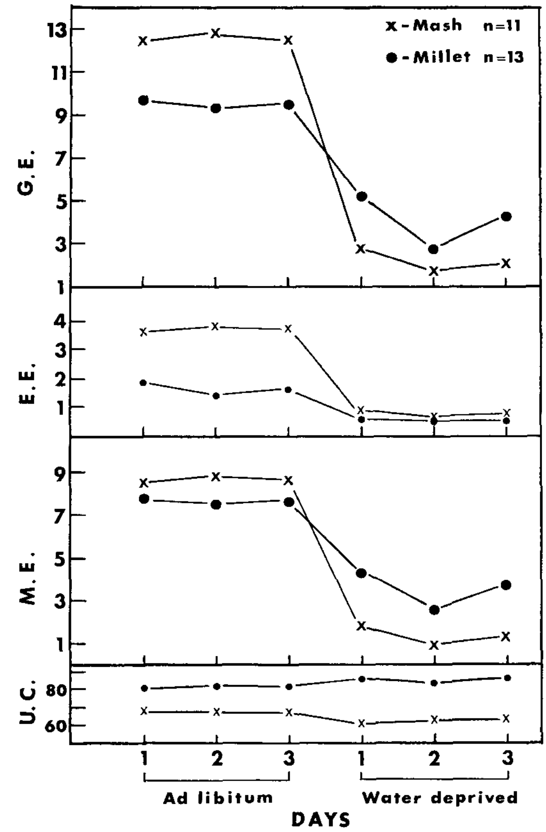

FIGURE 3. Initial effects of water deprivation on energy balance of Chipping Sparrows maintained on mash (X) and millet (O) diets. G.E. = Gross Energy Intake; E.E. = Excretory Energy Output; M.E. = Metabolizable Energy. All energy values in Kcal/bird/day. U.C. = Utilization Coefficient as %/bird/day.

The relationship between metabolizable energy ingested and water consumed with a diet of mash or millet is illustrated in figure 2. As water consumption decreased, a corresponding reduction in metabolizable energy occurred. The slopes of the regression lines for these diets are virtually identical (millet = 1.200, mash = 1.202), so that the magnitude of change in metabolizable energy per milliliter of water ingested each day was similar. However, the regression line for the millet diet was located above the regression line for the mash diet as a result of a higher mean metabolizable energy (5.91 Kcal) and a lower mean water consumption (1.6 ml) for millet-fed birds.

Figure 3 illustrates how water deprivation altered the daily energy values and utilization coefficients for each experimental group. During the 3-day period of ad libitum water consumption, the gross energy intake, excretory energy output, and metabolizable energy were higher for mash-fed birds than birds fed millet. However, the utilization coefficient was higher for birds on the millet diet. When water deprivation began, gross energy intake of the mash-fed birds decreased from about 12.4 to 2.8 Kcal/bird/day, while the intake for birds on the millet diet decreased less drastically from about 9.5 to about 5.2 Kcal/bird/day. The excretory energy output declined to about equal levels for both groups with deprivation. However, the overall decline was greater for mash-fed birds (from 3.8 to 0.7 Kcal/bird/day) than birds fed millet (from 1.8 to 0.65 Kcal/bird/day). As a result of the low excretory energy output and higher gross energy intake, the group fed millet had a higher metabolizable energy (3.5 Kcal/bird/day) during deprivation than the group fed mash (1.3 Kcal/bird/day).

The utilization coefficient for the group on mash decreased from about 69% on ad libitum water to about 64% during deprivation. However, for the group on millet, there was a slight increase in the coefficient from about 81 to 84% during deprivation.

PROLONGED EFFECTS OF WATER DEPRIVATION ON ENERGY INTAKE

Figure 4 illustrates the energy calculations and utilization coefficients for birds fed millet during a 21-day period without water. Data for the 3 days on ad libitum water and initial 3 days of water deprivation are the same as in figure 3. As the length of time without water increased, the four surviving birds increased their food intake to levels similar to those prior to deprivation while maintaining a reduced excretory energy output. Consequently, the utilization coefficient increased from about 82 to 90% with prolonged deprivation.

DISCUSSION

A comparison of ad libitum water consumption and energy intake values of Chipping Sparrows maintained on mash and millet diets indicates that mash-fed birds had higher water requirements than millet-fed birds. According to the ad libitum water consumption-body weight curve of Bartholomew and Cade (1963), the ad libitum intake of water for a 12-g Chipping Sparrow was expected to be about 30% of the body weight per day. However, Chipping Sparrows maintained on millet had an ad libitum water intake 5% less than the predicted value, whereas mash-fed birds consumed almost twice as much water as millet-fed birds. Likewise, during ad libitum water consumption, the gross energy intake and the excretory energy output of mash-fed birds were higher than millet-fed birds, indicating a higher turnover rate of the mash food. When given restricted amounts of water (2 and 4 ml), mash-fed birds showed an initial decline in energy intake and body weight, whereas millet-fed birds did not lose weight and exhibited only a slight decline in energy intake. When completely deprived of water, both groups immediately reduced their energy intake; however, mash-fed birds exhibited a sharper decline. After the first day, mash-fed birds showed a 77% reduction in gross energy intake as opposed to only a 45% reduction for millet-fed birds. None of the mash-fed birds was able to maintain body weight or survive prolonged water deprivation, whereas some members of the millet group stabilized their weight and survived water deprivation for at least 21 days. It is apparent that the weight losses which occurred during the initial stages of water deprivation were due not only to water loss but also to cessation of feeding.

Commercial mash, such as Purina Startena, has a gritty texture and a higher nitrogen (Morrison 1949; Blem 1968) and salt content

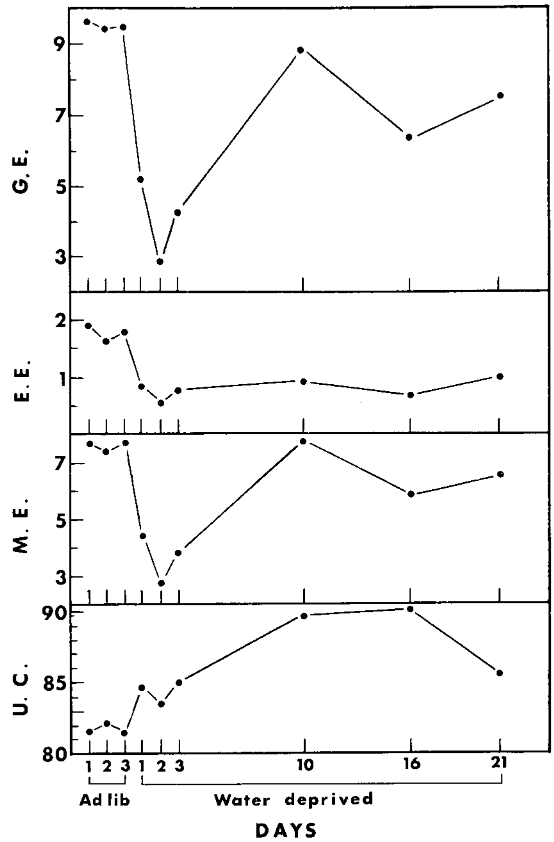

FIGURE 4. Effects of prolonged water deprivation on energy balance of millet-fed Chipping Sparrows. Symbols are same as in figure 3. Sample size was 13 during ad libitum water consumption and first 3 days of deprivation; 4 during remaining period.

than millet (personal analysis), all of which contribute in varying degrees to a higher water requirement. Ad libitum water consumption and total nitrogen excretion are increased with increased dietary protein content (McNabb et al. 1972). High ad libitum water consumption values have been reported for the White-crowned Sparrow (*Zonotrichia leucophrys*) (MacMillen and Snelling 1966), Sage Sparrow (*Amphispiza belli*) (Moldenhauer and Wiens 1970) and the Oregon Junco (*Junco oreganus*) (Anderson 1970), all of which were maintained exclusively on mash. These birds were unable to survive water deprivation for any extended period of time. Mash is a nutritious diet that allows granivorous birds to remain healthy. However, because of its high nitrogen and salt content and possibly other relatively indigestible constituents, mash apparently requires more water for ingestion, digestion, and excretion. This requirement can complicate estimates of minimal needs for water, and should be taken into account in the design of future studies of avian water metabolism.

Some investigators have used mixed diets of millet and mash (e.g., Ohmart and Smith 1971). Perhaps if the White-crowned Sparrow, Sage Sparrow, and Oregon Junco were maintained on a mixed diet, they would have fared better during water deprivation. Chipping Sparrows on a mixed diet had an ad libitum water intake only slightly higher than millet-fed birds, possibly due to the specific selection of millet seeds over mash. However, none of the five birds survived water deprivation for more than a week.

A reduction in food consumption during water deprivation has been reported for the Stark's Lark (*Spizocorys starki*), Grey-backed Finch-Lark (*Eremopterix verticalis*) (Willoughby 1968), and, at least in the initial stages of water deprivation for the Barbary Dove (*Streptopelia risoria*) (McFarland and Wright 1969) and Sage Sparrow (Moldenhauer and Wiens 1970). Apparently, some birds, such as the Budgerygah (*Melopsittacus undulatus*) (Cade and Dybas 1962), do not reduce their food intake during deprivation, and according to Calder (1964), the Zebra Finch (*Taeniopygia castanotis*) increased its food intake slightly on restricted water regimes. Ohmart and Smith (1970, 1971) have reported reduced food intakes for water-deprived Brewer's Sparrows (*Spizella breweri*) and Vesper Sparrows (*Pooecetes gramineus*). However, their conclusions are based on reduced defecation rates and not on actual food consumption values. Chipping Sparrows reduced their gross energy intake and excretory energy output during the initial stages of water deprivation regardless of diet. However, after an initial decrease in food intake, the water-deprived birds which survived 21 days on millet increased their food intake almost to the level consumed when ad libitum water was available while maintaining a low excretory energy output. The near normal intake of food plus the sustained lower excretory output resulted in a utilization coefficient which was about 8% higher than the utilization coefficient for birds on ad libitum water. The lower excretory output may be due to the longer retention of food in the alimentary tract for reabsorption of water which results in additional assimilation of food.

To maintain a dietary water balance, water intake with food ingestion must equal water lost through excretion (Bartholomew 1972). On a dry diet without drinking water, cloacal water loss must be reduced to offset the lower water intake. Cloacal water loss can be reduced by fecal water reabsorption and urinary concentration. A reduction in water content of fecal droppings from about 80 to 50% with water deprivation has been reported for several species (Calder 1964; Smyth and Bartholomew 1966; Moldenhauer and Wiens 1970; Ohmart and Smith 1970, 1971). Although the water content of Chipping Sparrow fecal droppings was not measured, visual examination suggested a reduced water content. However, a reduction in cloacal water loss in the Chipping Sparrow was due not only to a lowering of moisture content but also to a reduction in total excrement output. This same situation has been reported for the Sage Sparrow (Moldenhauer and Wiens 1970) and was apparent in the Brewer's Sparrow (Ohmart and Smith 1970) and the Barbary Dove. In the latter species, McFarland and Wright (1969) have shown that cloacal water loss during water deprivation is a linear function of food intake and suggest that the depression of food intake during water deprivation is a major means of water conservation. This linear relationship was evident in the initial stage of water restriction and water deprivation of Chipping Sparrows (fig. 2 and table 3). However, some millet-fed birds after the third day of deprivation increased their gross energy intake while sustaining a lowered excretory output. Therefore, the reduced cloacal water loss was sustained by a decrease in amount and water content of excreta but not at the expense of a continued reduced energy intake.

The eastern Chipping Sparrow occupies a mesic environment and probably satisfies its water requirements with surface water, succulent vegetation, and insects found in the habitat. However, temporary droughts could initiate food inhibition which would initially conserve water by reducing the cloacal water loss until another water source is found, and allow for physiological adjustments whereby near normal food consumption can be resumed while maintaining a lowered excretory output. Furthermore, the resultant higher percentage of available energy would require less foraging time during water scarcity.

So far the Chipping Sparrow is the only mesophilic species tested that can survive on a dry diet without drinking water. This ability may be explained in the close relationship of *Spizella passerina* to the desert-inhabiting *Spizella breweri* (Mayr and Short 1970).

ACKNOWLEDGMENTS

We are indebted to A. A. Dewees for his help with the statistical analysis of the data and to W. R. Dawson and R. D. Ohmart for their critical reading of the manuscript. This research was supported in part by grants from the Society of Sigma Xi and Chapman Memorial Fund.

LITERATURE CITED

ANDERSON, S. 1970. Water balance of the Oregon Junco. Auk 87:161–163.

BARTHOLOMEW, G. A. 1972. The water economy of seed-eating birds that survive without drinking, p. 237–254. *In* K. H. Voous [ed.] Proc. XV Int. Ornithol. Congr. E. J. Brill, Leiden.

BARTHOLOMEW, G. A., AND T. J. CADE. 1956. Water consumption of House Finches. Condor 58:406–412.

BARTHOLOMEW, G. A., AND T. J. CADE. 1963. The water economy of land birds. Auk 80:504–539.

BARTHOLOMEW, G. A., AND W. R. DAWSON. 1954. Body temperature and water requirements in the Mourning Dove, *Zenaidura macroura marginella*. Ecology 35:181–187.

BLEM, C. 1968. Determination of caloric and nitrogen content of excreta voided by birds. Poultry Sci. 47:1205–1208.

CADE, T. J., AND J. A. DYBAS, JR. 1962. Water economy of the Budgergah. Auk 79:345–364.

CALDER, W. A. 1964. Gaseous metabolism and water relations of the Zebra Finch, *Taeniopygia castanotis*. Physiol. Zool. 37:400–413.

KING, J. R. 1961. The bioenergetics of vernal premigratory fat deposition in the White-crowned Sparrow. Condor 64:128–142.

MACMILLEN, R. E., AND J. C. SNELLING. 1966. Water economy of the White-crowned Sparrow and its use of saline water. Condor 68:388–395.

MAYR, E., AND L. L. SHORT. 1970. Species taxa of North American birds. Publ. Nuttall Ornithol. Club, No. 9, 127 p.

MCFARLAND, D., AND P. WRIGHT. 1969. Water conservation by inhibition of food intake. Physiol. Behav. 4:95–99.

MCNABB, F. M. A., R. A. MCNABB, AND J. M. WARD. 1972. The effects of dietary protein content on water requirements and ammonia excretion in pigeons, *Columba livia*. Comp. Biochem. Physiol. 43:181–185.

MOLDENHAUER, R. R., AND J. A. WIENS. 1970. Water economy of the Sage Sparrow, *Amphispiza belli nevadensis*. Condor 72:265–275.

MORRISON, F. 1949. Feeds and feeding. Morrison, New York, p. 1122–1123.

OHMART, R. D., AND E. L. SMITH. 1970. Use of sodium chloride solutions by the Brewer's Sparrow and Tree Sparrow. Auk 87:329–341.

OHMART, R. D., AND E. L. SMITH. 1971. Water deprivation and use of sodium chloride solutions by Vesper Sparrows. Condor 3:364–366.

POULSON, T. L., AND G. A. BARTHOLOMEW. 1962. Salt balance in the Savannah Sparrow. Physiol. Zool. 35:109–119.

SMYTH, M., AND G. A. BARTHOLOMEW. 1966. The water economy of the Black-throated Sparrow and the Rock Wren. Condor 68:447–458.

WILLOUGHBY, E. J. 1968. Water economy of the Stark's Lark and Grey-backed Finch-Lark from the Namib Desert of Southwest Africa. Comp. Biochem. Physiol. 27:723–745.

Accepted for publication March 30, 1973.