WATER ECONOMY OF THE BUDGERYGAH

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BECAUSE water is the universal solvent in which the biochemical re-
actions of metabolism occur, it is an essential constituent of living organ-
isms and one of the most necessary to life of all environmental resources.
A basic problem of animal life is to maintain the required concentrations
of water within the organism. To solve this problem terrestrial animals
have had to evolve mechanisms for preventing an excess loss of water and
for using efficiently the water available in their environment. No ter-
restrial environment is more demanding of these adaptive features than
the deserts, and yet a surprising number and variety of animals live under
harsh desert conditions of high temperature and low humidity, the two
physical factors that most aggravate the problems of water economy for
terrestrial organisms. Chew's (1961) recent review of the physiological
adaptations of desert-inhabiting vertebrates for water regulation should
be consulted for pertinent details.

The most critical avian species for study are small sparrows and finches
that live on a diet of dry seeds, which provide little free water. Many
seed-eating birds of arid habitat seem not to have evolved special physio-
logical mechanisms of water conservation comparable to those of desert
rodents such as kangaroo rats and pocket mice, which can live on "meta-
bolic water" (Bartholomew and Cade, 1956). Such rodents can survive
indefinitely on dry seeds without drinking (Schmidt-Nielsen and Schmidt-
Nielsen, 1952). Most species of birds must drink or eat succulent foods
in order to survive in the desert, and consequently desert bird populations
tend to be concentrated around water holes. Furthermore, the smaller the
bird, the more acute is its need for water, because small birds lose propor-
tionately more water from their lungs in the process of breathing than
large birds. A critical upswing in the curve relating body weight to rela-
tive water loss occurs at a body weight of about 50 g (Bartholomew and
Dawson, 1953), and here also one observes an upswing in weight-relative
water consumption (Bartholomew and Cade, 1956).

Studies by Cade and Bartholomew (1959) on several races of Savannah
Sparrows (*Passerculus sandwichensis*) indicated that a small, seed-eating
bird can be relatively independent of a source of drinking water for con-
siderable periods of time. In particular, one of the salt-marsh races, *P.
s. rostratus,* showed a remarkable ability to survive long periods of water
deprivation without serious loss of body weight. The performance of this
bird stimulated a search for other species that might be similarly adapted
to desert conditions with a minimum intake of water. The Australian
Budgerygah or Grass Parakeet (*Melopsittacus undulatus*), a xerophilous

seedeater weighing around 30 g, appeared to be a useful subject. Wild Budgerygahs exist in vast numbers in arid, interior Australia (Barrett, 1945; Watmough, 1954; Chisholm, 1958), and aviculturists have long noted that domesticated Budgerygahs drink little by comparison with other seedeaters such as finches or canaries.

MATERIALS AND METHODS

Ten adult, domesticated Budgerygahs were subjected to various experimental conditions to obtain information about their water economy. The primaries of each bird were clipped for convenience in handling. The birds were housed individually in wire cages measuring $25 \times 25 \times 25$ cm ($10 \times 10 \times 10$ inches), and they were fed the Hartz Mountain Parakeet food mixture of millet and canary seeds. A constant photoperiod of 12 hours of artificial light and 12 hours of darkness was used in all experiments. The amount of water drunk by each bird was measured with graduated cylinders equipped with "L"-shaped glass drinking tubes of a design first used by Bartholomew and Dawson (1954). With such an apparatus the daily fluid consumption can be measured with an accuracy of about 0.5 ml. Daily food consumption was monitored in several experiments by determining the difference in weight of the food container before and after each light period and subtracting from this figure the weight of the chaff and spilled seeds on a removable tray in the bottom of each cage. These weights were made with an accuracy of 0.1 g. The daily dry-weight production of excrement (renal and bowel products combined) was determined for five birds for 10 days by removing and weighing to 0.01 mg the accumulation of droppings in the cage each day. In three experiments the water content of a sample of 20 droppings was estimated by weighing fresh droppings as soon as they were voided, then drying them in an oven to a constant weight to obtain the difference. These weights were also determined to an accuracy of 0.01 mg.

Respiratory (pulmocutaneous) water loss was measured for five birds by a slight modification of the method used by Bartholomew and Dawson (1953), which employs anhydrous magnesium perchlorate, $Mg (ClO_3)_2$, as the agent for picking up water introduced by the bird into a system of flowing, dry air. Air flow was maintained at 350 ml/min through a transparent glass chamber in which the bird could be observed. A cotton plug was placed in the cloaca just before each run to prevent the bird from voiding excrement during the measurement of respiratory water loss. The relative humidity during each run was approximated by taking wet-bulb and dry-bulb temperatures inside the chamber before and after the bird was placed in the chamber and obtaining the difference between the calculated relative humidities.
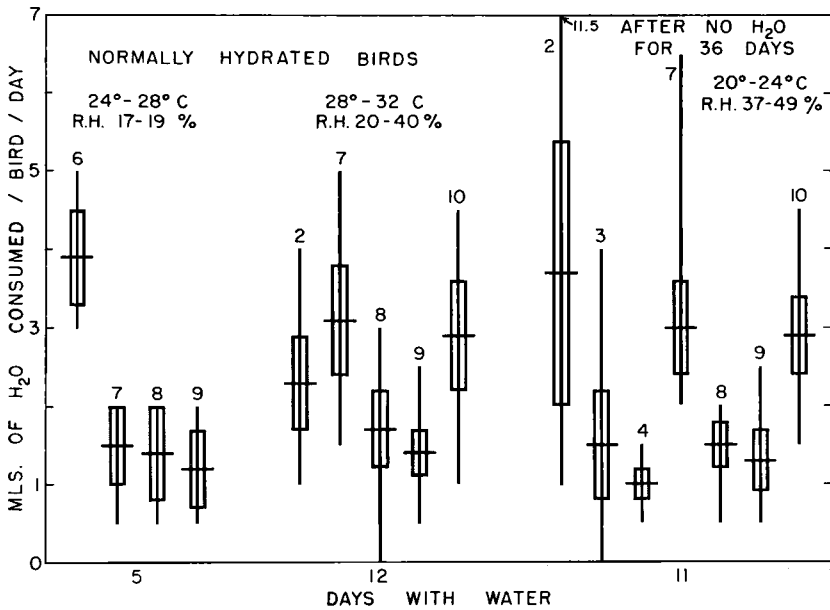
Figure 1. Drinking responses of individual Budgerygahs under various conditions of temperature, humidity, and prior access to water. Numbers designate specific birds. The vertical lines represent the observed range; the horizontal lines indicate the means (M); the rectangles indicate the interval $M + 2\sigma_m$ to $M - 2\sigma_m$. N equals the number of days during which the consumption of water was measured. Normally hydrated birds had unlimited access to water for several weeks before measurements were made, for five days in the first group and for 12 days in the second. Water consumption was measured for 11 days following dehydration in the third group.

The birds were weighed near the end of the dark period to obtain an indication of their ability to maintain themselves in water balance under the experimental conditions imposed on them. Ambient temperature and relative humidity could not be controlled, but they were measured two or more times each day during the experiments. By utilizing different sections of a long corridor in a subbasement where a permanent temperature gradient existed from one end to the other, it was possible to keep birds at various temperatures ranging between averages of 20 and 30° C with daily variations of less than five degrees. Relative humidity was more variable.

<div align="center">RESULTS</div>

Effect of ambient temperature and deprivation of water on drinking. Figure 1 compares the drinking responses of three groups of birds as follows: four normally hydrated birds kept at moderate temperatures and

humidities, a second group of five normally hydrated birds kept at an average temperature of 30° C, and a third group of seven individuals that had been kept without water for 36 days before they were allowed to drink. The first point to note is the considerable individual variability that exists among these birds. Such variation in drinking is to be expected in any population of birds. Some individuals (birds 6, 2, and 10) can be classified as "drinkers," while others (3, 4, 8, and 9) are "nondrinkers."

At temperatures of 24 to 28° C and relative humidities of 17 to 19 per cent, bird number 6, a small, weak individual weighing about 25 g, drank an average amount of water equivalent to 15 per cent of body weight per day. This value is close to the average for many other seed-eaters of comparable size (Bartholomew and Cade, 1956), but numbers 7, 8, and 9—more robust individuals weighing around 30 g—drank an amount of water equivalent to only 5 per cent of body weight per day. Such low daily consumptions are not reported for any other seedeating species of comparable size. Water consumption appears to increase slightly when Budgerygahs are kept at higher temperatures, but even for the drinkers the values do not exceed 10 per cent of body weight per day, and in the case of nondrinkers such as numbers 8 and 9 there is really no significant increase in fluid consumption over the range from 20 to 30° C.

The same low consumptions obtain after Budgerygahs have been kept without water. High consumptions may occur in the first day or two after a period of dehydration, as in the case of birds 2 and 7, both of which lost considerable weight without water; but birds such as numbers 4, 8, and 9, which maintained their weights without water, showed no tendency to increase their consumption of water when it was again made available.

Effects of saline solutions on drinking. Figure 2 summarizes some data on the consumption of dilute salt solutions by Budgerygahs. When offered 0.2 M or 0.3 M NaCl as their only source of drinking water, individual Budgerygahs showed one of two distinct responses: drinkers increased their fluid consumption, but the nondrinkers decreased fluid consumption to trace amounts. When returned to distilled water, the drinkers continued to drink about the same volumes as before, while the nondrinkers continued to drink little or no water. In general the drinkers lost weight on the salt solutions, and three of them died—numbers 1 and 6 after reducing fluid consumption, and number 5 after a very high intake of saline water—while the nondrinkers held their weights.

Food consumption in relation to ambient temperature and the presence or absence of water. In an over-all consideration of water economy, food consumption must be taken into account, because all foods contain some
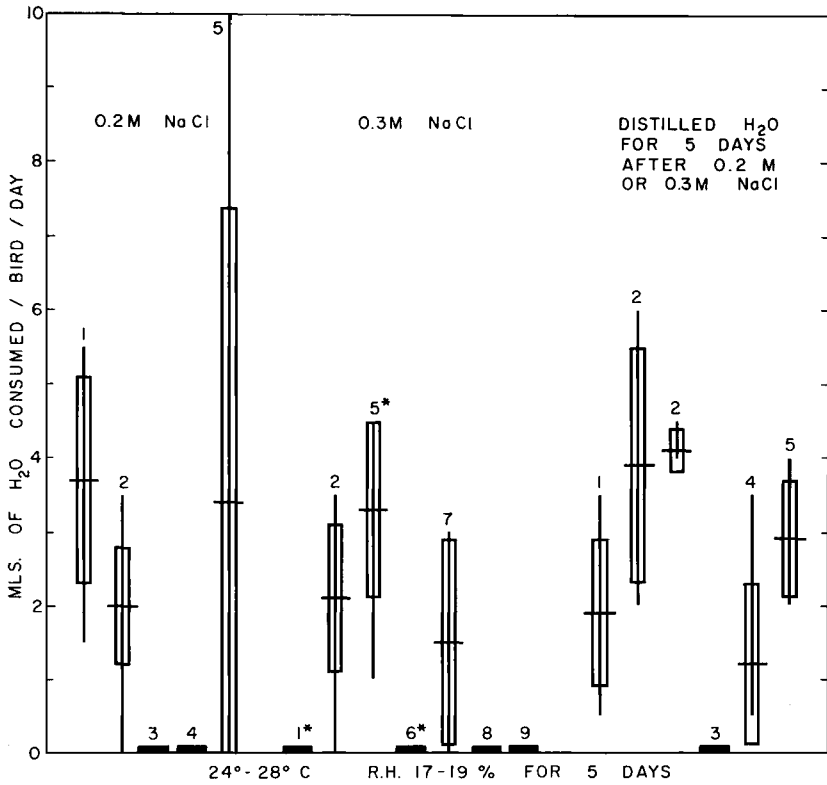
Figure 2. **Influence of salt on drinking responses of Budgerygahs. Statistical symbolism same as in Figure 1. Black bars indicate unmeasured, trace quantities, and asterisks mark individuals that died during the experiments. Measurements were made for five days in all cases.**

free water and because organisms derive physiologically useful water from the metabolism of their food stuffs. Figures 3, 4, 5, 6, and 7 show daily food consumptions and body weights for three drinkers and two non-drinkers kept under five successively different experimental conditions. In the case of bird number 2 (Figure 3), a drinker, the average food consumption was equivalent to slightly less than 19 per cent of the average body weight per day in experiment A without water. In experiment B under similar conditions of temperature and humidity but with drinking water available, the bird gained in weight, although the food consumption decreased slightly to an average value equivalent to a little more than 18 per cent of body weight per day. In experiment C with water still present but at a higher air temperature averaging 30° C, the bird's weight dropped, and its food consumption decreased still more to an average equivalent
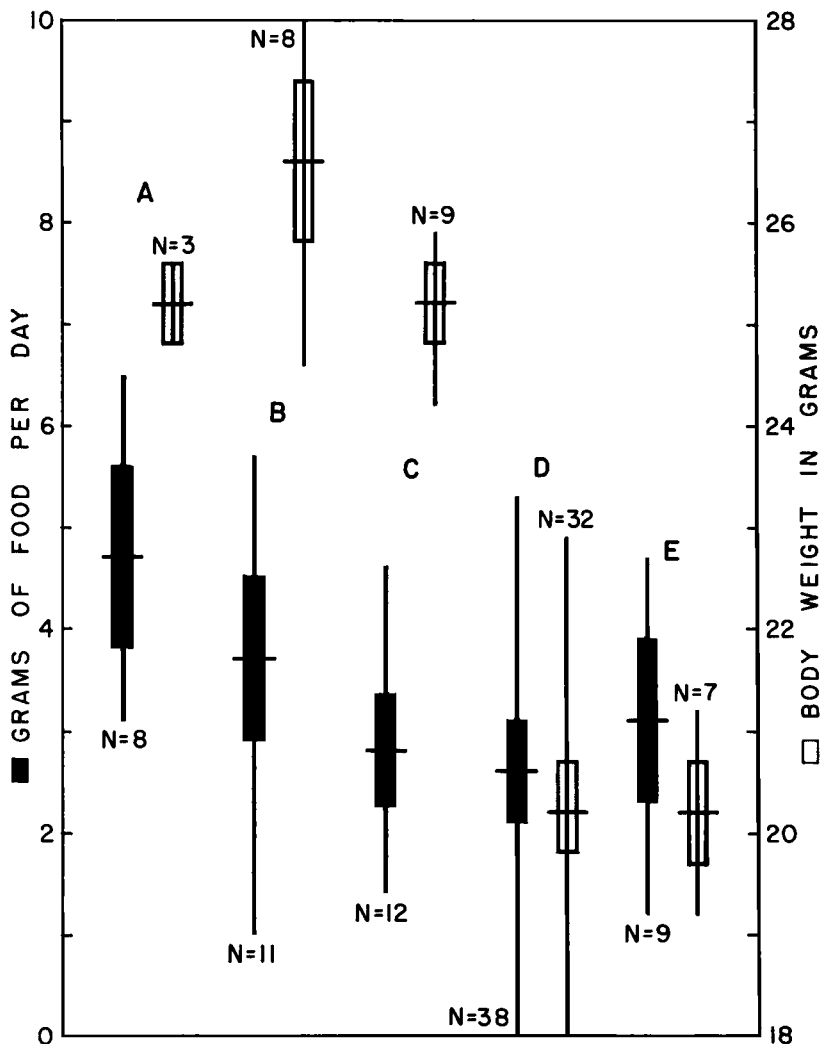
Figure 3. Daily food consumption and body weight in relation to temperature and the presence or absence of drinking water for bird number 2, a drinker. Statistical symbolism same as Figure 1. In experiment A, the bird was without water at 23 to 25°C and relative humidity of 36 to 45 per cent; in experiment B, the bird was allowed to drink ad libitum at 20 to 24°C and relative humidity of 37 to 49 per cent; in experiment C, the bird drank ad libitum at 28 to 32°C and relative humidity of 22 to 30 per cent; in experiment D, the bird was without water at 28 to 32°C and relative humidity of 25 to 36 per cent; and in experiment E, the bird was without water at 22 to 25°C and relative humidity of 32 to 42 per cent.

to about 12 per cent of body weight. In experiment D without water for 38 days at a high range of air temperature, food consumption became much more variable from day to day but still averaged about three g per day; but body weight dropped very sharply to an average of 20 g, so that the average food consumption was equal to 15 per cent of body weight per day. Returned to a milder temperature but still without water in experiment E, the bird increased its food consumption slightly, and although the average body weight remained the same as in the previous experiment, there was in fact a significant increase in weight over the terminal values of experiment D.

The data for birds 7 and 10 are similar (Figures 4 and 5). Again note the decreased food consumption at high air temperatures whether water was present or absent, the significant loss in body weight when deprived of water, and the increase in food consumption when the birds were returned to milder temperatures and the consequent holding of body weight.

The performances of the two nondrinkers under the same set of conditions were somewhat different from those of the drinkers (Figures 6 and 7). Food consumption varied little from an average of four g per bird per day regardless of experimental conditions, and there were relatively slight changes in body weight. Again, the set of weights for experiment E, although averaging less than the over-all average for experiment D, actually constituted an increase in weight over the terminal weights of the former experiment. All five birds, to some degree, showed depressed food consumptions at high air temperatures whether water was present or not and an increase in food consumption as soon as air temperature dropped.

The temporal course of changes in body weight and food consumption for the same five birds held for 38 days without water is shown in Figure 8. Bird number 2, which was always a light, weak individual, showed the greatest fluctuation in body weight and great variations in daily food consumption, from nothing on one day to more than 25 per cent of body weight on another. The really significant point about number 2 is that after losing as much as five g of body weight over a period of 20 days, by suddenly increasing its daily food consumption to values ranging between 15 and 25 per cent of body weight per day, it was able to reverse this downward trend and regain most of the weight it had lost. This ability to reverse a serious loss in weight during a period of water deprivation solely by increasing the consumption of dry seeds is peculiar to Budgerygahs among the small birds so far studied. The other four birds maintained a rather uniform food consumption ranging between 10 and 15 per cent of body weight per day, while their body weights drifted downward slightly over the 38-day period.

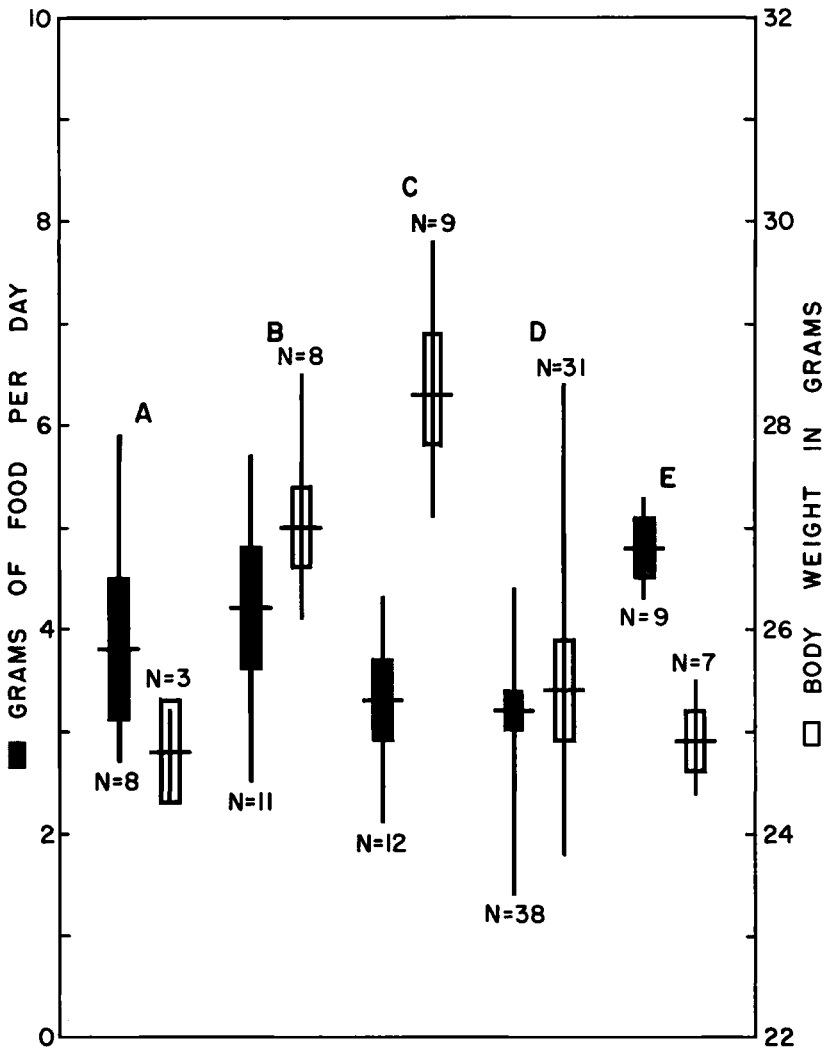Birds 2 and 9 were continued without water for a total period of 130

Figure 4. Daily food consumption and body weight in relation to tempera-
ture and the presence or absence of drinking water for bird number 7, a
drinker. Symbolism and experimental conditions same as Figure 3.

days. During the last 60 days they were kept at a constant temperature
of 20° C and relative humidity averaging 30 per cent. They gained weight
and completed a full molt during this terminal period.

Water loss from excrement. To survive for long periods without drink-
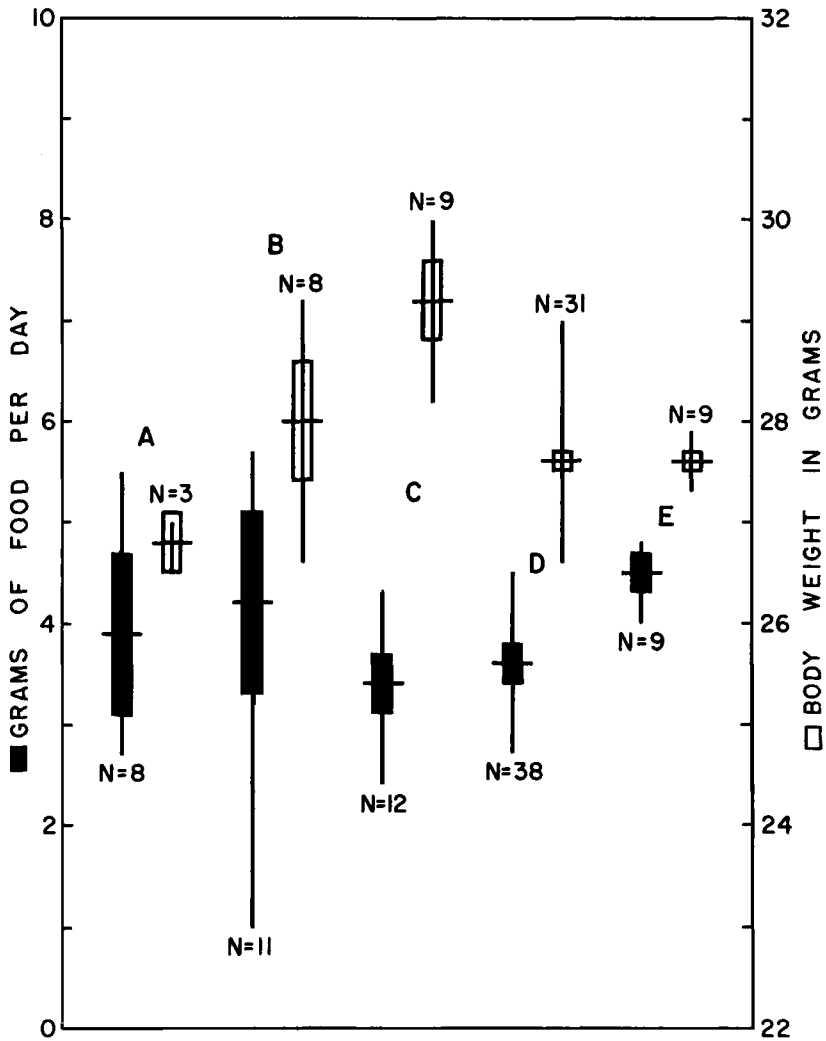ing, a bird must possess mechanisms for conserving water. Table 1 com-

Figure 5. Daily food consumption and body weight in relation to tempera-
ture and the presence or absence of drinking water for bird number 10, a
drinker. Symbolism and experimental conditions same as Figure 3.

pares the concentration of water in the excreta of hydrated birds with
that in the excreta of dehydrated birds. Normally hydrated Budgerygahs
with drinking water produced an excrement that was at least 75 per cent
water. Because of the difficulty of collecting these very wet droppings,
some of the water was lost before weighing, so that a true value is prob-
ably closer to 80 per cent. When the birds were without water for a

number of days, the excrement became much drier and averaged only about 60 per cent water or less. The average dry weight of the daily production of excrement for five birds kept without water at 20 to 25° C and a relative humidity of 20 to 40 per cent is shown in Table 2. The over-all average for the five birds is 436.8 mg per day. Assuming a 60 per cent water content for the wet weight, one can calculate that the average daily loss of water from excrement amounts to about 655 mg per bird.

Evaporative water loss. Table 3 summarizes data on pulmocutaneous water loss. Even when Budgerygahs were naturally asleep or drugged lightly with a sleep-inducing hypnotic such as paraldehyde, their rates of evaporative water loss were equivalent to a total daily loss of one to two g of water under the conditions of the experiment. A little activity abruptly increased the rate of loss to values equivalent to a daily loss of 2 to 3.5 g of water.

DISCUSSION

Relation of water loss to metabolism. Many small, granivorous birds survive for only a few days without water to drink. The main reason for this quick, lethal dehydration is a high rate of respiratory water loss, which cannot be compensated by metabolically produced water plus the free water in their food, as in the case of some heteromyid rodents. Besides possessing other well-known water-conserving mechanisms, *Dipodomys merriami*, for example, evaporates only 0.46 to 0.61 mg H_2O/ml oxygen consumed in very dry air at room temperature (Schmidt-Nielsen and Schmidt-Nielsen, 1950), whereas a bird like the Cardinal (*Richmondena cardinalis*), which weighs about 40 g, evaporates 0.9 mg H_2O/ml oxygen consumed under basal metabolic conditions (Dawson, 1958). This latter value, which is equivalent to a total daily loss of about 2.4 g of water, or 6 per cent of body weight per day, and which is almost twice the amount of metabolic water produced in the same period of time, is similar to that found for several other species of birds in the same size range (Bartholomew and Dawson, 1953). Because of the unfavorable difference between evaporative water loss and metabolic water production generally existing in small birds, the long survival without drinking of species such as *Passerculus sandwichensis* (Cade and Bartholomew, 1959) and *Melopsittacus undulatus* is both surprising and challenging in its implications for adaptive adjustments of respiratory water loss, metabolic rate, and body temperature to a low influx of water.

The culmination of these adjustments has to be a decrease in the amount of water lost per milliliter of oxygen consumed and per milliliter of metabolic water produced. A favorable balance between respiratory loss

and metabolic production of water could be brought about conceivably by a reduced metabolic rate and lowered body temperature, which would result in a somewhat cooler expired air with less moisture-carrying capacity than is typical of birds with their usually high body temperatures. The summer-time torpor of small desert rodents such as *Perognathus* (Bartholomew and Cade, 1957) and *Microdipodops* (Bartholomew and MacMillen, 1961) is undoubtedly advantageous in reducing respiratory water loss, but birds typically respond to daytime desert conditions by an elevation of body temperature and metabolic rate (Dawson, 1954). Pulmonary water loss might also be reduced by modification of the pattern of breathing to increase the ratio of alveolar air to dead air (Chew, 1961), thereby increasing the efficiency of gaseous exchanges per volume of expired air. Finally, the ratio between the volume of expired air and metabolic rate, and the contingent ratio between respiratory water loss and metabolic water production, could be reduced by more efficient mechanisms for gaseous exchanges between the circulatory system and the alveolar air (increased haemoglobin content of blood, for example).

Although our data do not include measurements of metabolic rate or body temperature, we can nevertheless attempt some inferences about the adjustments that Budgerygahs make in order to remain in water balance in the absence of drinking water.

Water budget of a nondrinking Budgerygah. Consider a 30-g Budgerygah with an average daily food consumption of four g of seeds. These seeds contain about 10 per cent free water under the conditions of temperature and humidity to which they were exposed during our experiments. Proteins constitute 12 per cent, fats 4 per cent, digestible carbohydrates about 53 per cent, indigestible cellulose fibers about 11 per cent, and ash about 10 per cent. If one assumes that the digestible energy component of the food (see Brody, 1945; King and Farner, 1961) includes all the proteins, fats, and digestible carbohydrates, then the metabolic water potentially available in the four g of food plus the free water equals two g or ml. The actually metabolized component will, however, be something less than the digestible energy component, and if one assumes that it is about 90 per cent (see Brody, 1945), then the metabolic water actually produced from the four g of food plus the free water equals about 1.844 g. Of this total available water, about 0.65 g are lost in the excrement, leaving only 1.19 g available for respiratory loss.

On the basis of the experimental values for pulmocutaneous water loss reported in Table 3, it is difficult to see how the Budgerygah can maintain itself in water balance on the four g of seeds. Since the bird can, in fact, do so for long periods of time, we conclude that most of our experimental
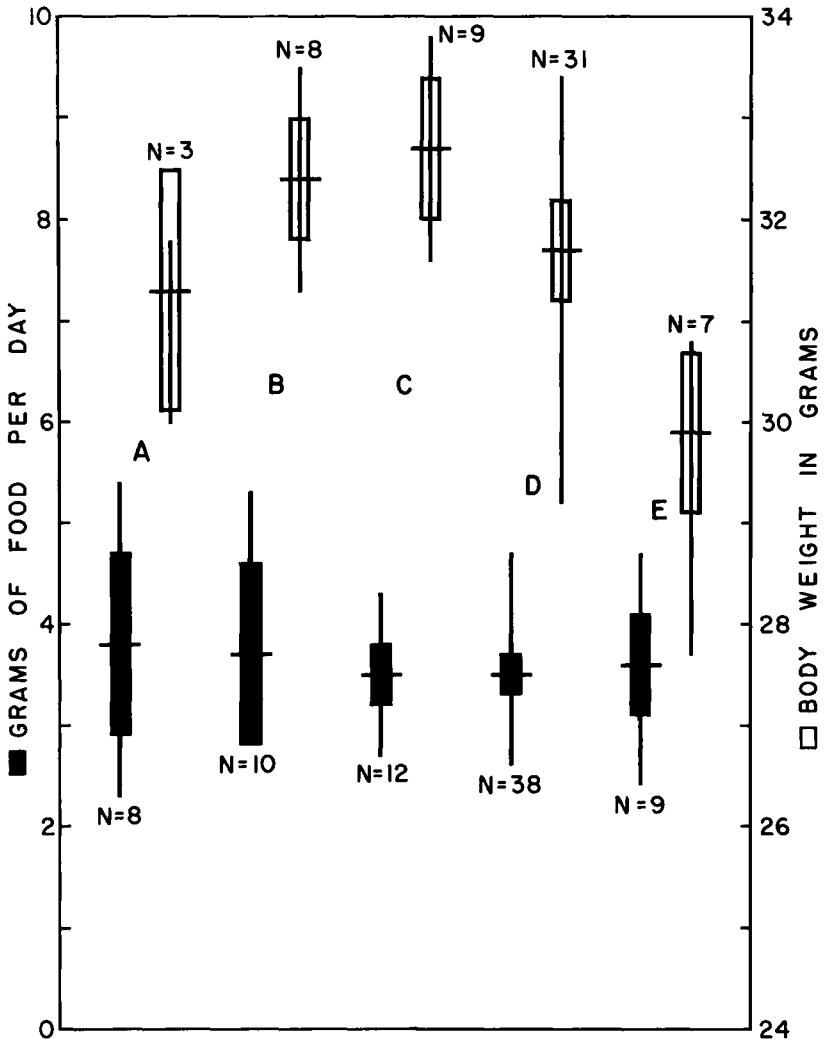
Figure 6. Daily food consumption and body weight in relation to temperature and the presence or absence of drinking water for bird number 8, a nondrinker. Symbolism and experimental conditions same as Figure 3.

values for pulmocutaneous water loss are somewhat too high, in spite of the fact that the over-all average of 8.8 per cent of body weight per day approaches closely the predicted value of 10 per cent derived from Bartholomew and Dawson's (1953) curve for weight-relative water loss. Although the birds were in a postabsorptive state, it may be that their metabolic rates were high because of their stressful confinement in a
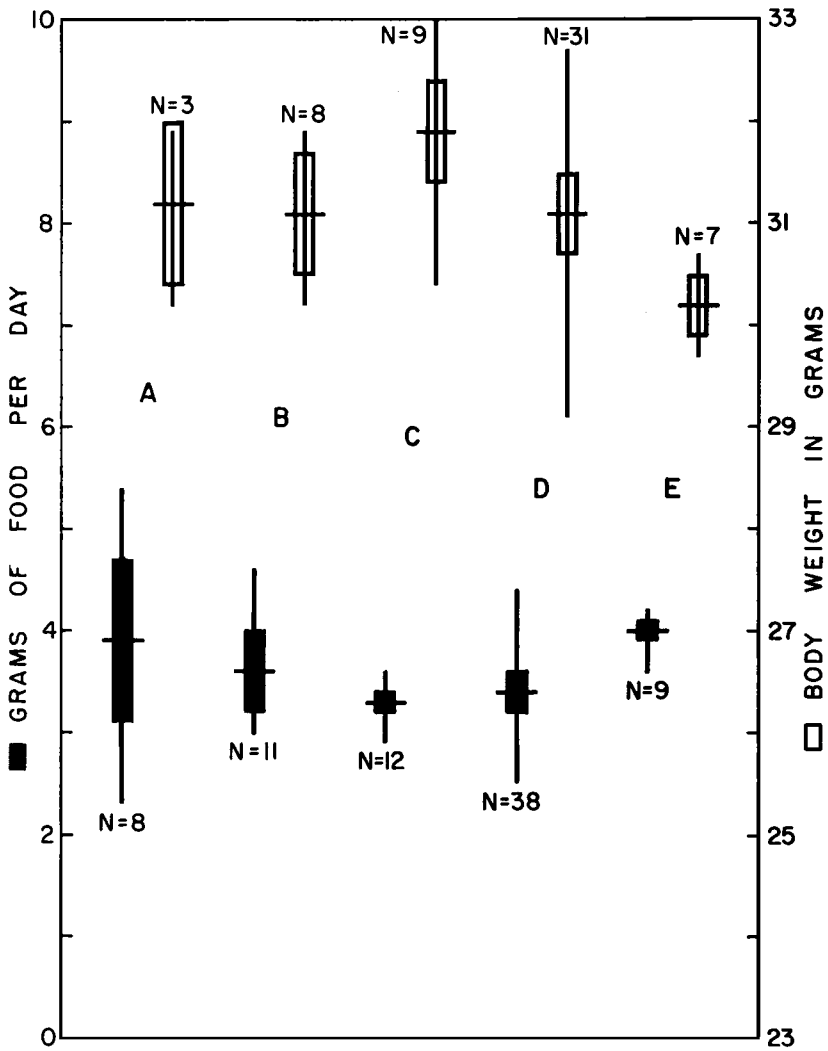
Figure 7. Daily food consumption and body weight in relation to tempera-ture and the presence or absence of drinking water for bird number 9, a nondrinker. Symbolism and experimental conditions same as Figure 3.

small container during the measurements. Further, the air temperature in these experiments averaged some 5° C below the lower limit of the thermal neutrality zone of the Budgerygah, as indicated by Giaja's data (in Davson, 1951: 123).

Even so, it is obvious from the data in Table 3 that much activity with its consequent increase in oxygen consumption would result in a net loss of
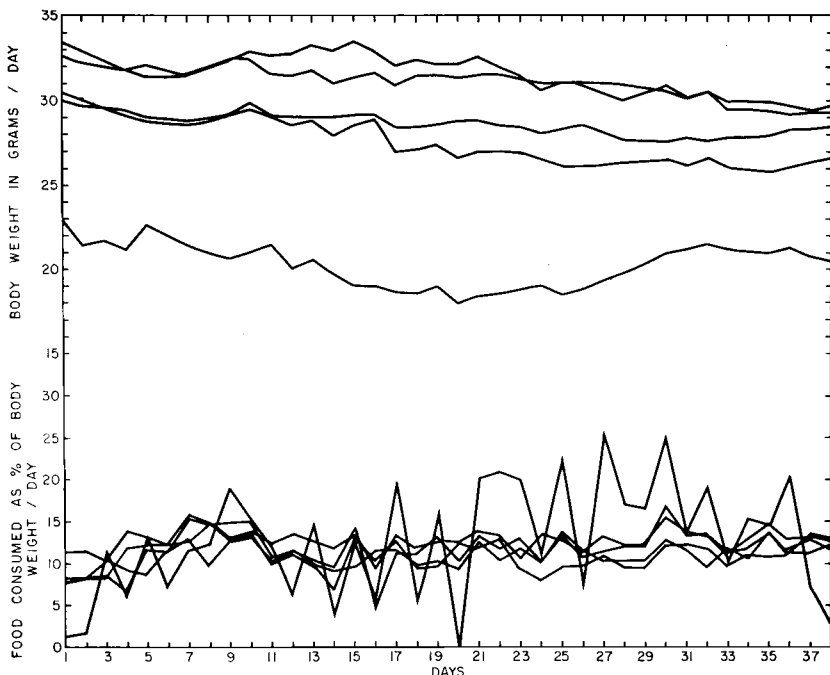
Figure 8. Time course of changes in body weight and food consumption for birds number 2, 7, 8, 9, and 10 held without water for 38 days.

water from the bird's tissues. A nondrinking Budgerygah, therefore, appears able to maintain itself in water balance only by remaining quiescent as much as possible. As a matter of observation, our Budgerygahs were often inactive in their cages for hours at a time, especially at higher air temperatures.

TABLE 1

WATER CONTENT OF THREE SAMPLES OF 20 BUDGERYGAH DROPPINGS

Experimental conditions	Wet weight of droppings in milligrams			Dry weight of droppings in milligrams			Percentage of water			
	Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.	S.E.
After 30 days without water at 20 to 25° C and 20 to 40% R.H.	3.1– 21.8	12.9	6.1	1.0– 11.8	5.2	2.9	45.9– 70.3	60.9	8.7	1.9
After 22 days without water at 28 to 32° C and 20 to 40% R.H.	6.3– 16.6	11.0	2.6	2.0– 6.9	4.3	1.6	50.5– 68.1	58.6	5.8	1.3
With drinking water at 20 to 25° C and 20 to 40% R.H.	7.8– 29.1	17.8	7.2	2.2– 6.9	4.4	1.6	63.9– 86.3	73.6	6.7	1.5

TABLE 2
DAILY PRODUCTION OF EXCREMENT (DRY WEIGHT) OF FIVE BUDGERYGAHS FOR 10 DAYS

Bird No.	Weight in milligrams per day		
	Maximum	Minimum	Average
2	666.55	392.30	523.4
3	568.60	226.60	433.4
4	516.80	260.60	349.9
8	465.75	389.60	435.1
9	518.80	334.15	435.1

A further advantage in maintaining its water balance without drinking may accrue from the fact that the Budgerygah seems to have a low basal metabolic rate for a bird of its size. From Giaja's data (see Brody, 1945; Davson, 1951) one can calculate that the basal metabolic rate of a 30-g Budgerygah is 6.69 kcal per day or 223 kcal/kg body weight/day. This rate is considerably lower than those reported for a number of other birds ranging in weight from 22 to 40 g (Brody, 1945; King and Farner, 1961). Since the four g of seeds eaten by the Budgerygah yield a metabolizable energy of about 10.9 kcal, of which an undetermined amount is lost in specific dynamic action, it is again apparent from these calculations that the domesticated Budgerygah does not maintain itself much above a resting metabolic level in the absence of water.

If one considers the six lowest values in Table 3 to represent measurements made under basal conditions, then the average figure of 1.86 g per day or 2.6 mg H_2O/gm/hr is still somewhat too high to balance with the figures for metabolic water production. If one assumes that the respiratory water loss is no greater than the water that can be derived from the daily food intake minus the water loss in excrement, then the respective

TABLE 3
SUMMARY OF PULMOCUTANEOUS WATER LOSS

Bird No.	Wt. in grams	Air temp.	Rel. hum.	Mgm. loss per hr.	Gram loss per day	% B.W. per day	Remarks
2	21.0	25.5	20	76.8	1.84	8.8	Alternately quiet and active
2	20.4	25.0	22	122.4	2.94	14.5	Wide awake and very active
7	26.0	26.5	15	75.0	1.80	6.9	Little movement, asleep some
7	27.1	26.0	22	117.6	2.82	10.3	Awake and mildly active
8	29.3	26.5	21	128.4	3.08	10.5	Awake and mildly active
8	30.4	25.5	38	114.6	2.29	7.5	Awake but no activity
8	31.4	20.0	31	76.2	1.83	5.5	Deep sleep from paraldehyde
8	31.4	20.0	31	93.7	2.25	7.1	Deep sleep from paraldehyde
9	29.9	25.5	28	85.8	2.06	6.9	Awake and mildly active
9	30.3	25.0	30	150.4	3.61	11.9	Constantly active
9	30.2	22.5	27	122.9	2.95	9.8	Drowsy from light paraldehyde
10	27.9	26.5	20	44.2	1.06	3.8	Quiet, asleep most of time
10	28.9	24.0	30	130.8	3.14	10.8	Active most of the time

values are 1.19 g per day or 1.7 mg H_2O/gm/hr. Since some body weight tends to be lost during a very long run without water, we suspect the real value lies somewhere between these two estimates, probably close to the lower figure. Simultaneous measurements of respiratory water loss and metabolic rate are needed for a precise expression of this relationship.

Our findings do suggest that the Budgerygah's ability to survive long periods of water deprivation is related somehow to a low daily production of heat. This low rate is brought about in part by a reduction in gross activity, but Giaja's data also point to the distinct possibility of a species-specific basal metabolic rate that is lower than that usually found in birds of comparable size. His data also indicate a zone of thermal neutrality lying above 32° C, and the fact that our birds ate less food at 30° than they did at lower temperatures (Figures 3–7) fits this picture. Since this is rather a high lower critical temperature (see summaries for birds by Dawson, 1954; King and Farner, 1961), it would be most interesting to know the upper critical temperature for the Budgerygah. From the standpoint of water economy, it would be distinctly advantageous for the bird to be able to maintain a low metabolic rate at ambient temperatures approaching 40° C. The highest upper critical temperature so far reported for small birds is 38° C (King and Farner, 1961). In the absence of simultaneously recorded data on oxygen consumption, body temperature, and respiratory water loss it is impossible to speculate further on the precise way in which lowered metabolism may be related to a decrease in respiratory water loss per unit of metabolic water produced in the Budgerygah. But it may involve the greater efficiency of energy utilization that occurs at a maintenance level of nutrition (Brody, 1945), for at a maintenance level there would seem to be less respiratory water lost per calorie of net energy obtained from the food than at any other nutritional level.

Ecology and evolution. The physiological relationships just considered make it unlikely that wild Budgerygahs exist in arid environments for many days without drinking, since in nature the birds must function at considerably above their basal metabolic rate with a consequently greater respiratory loss of water. The meager literature on the natural history of the species presents a picture of great flocks of Budgerygahs and other psittacines flying to scattered water holes in the xeric parts of Australia to drink at dawn or dusk (Barrett, 1945; Watmough, 1954; Chisholm, 1958). It does not seem to be known whether individual Budgerygahs regularly visit water at least once a day, but during the more severe periods of high temperature and low humidity they probably do.

A further indirect dependence upon water is shown by the fact that the reproductive periods of the Budgerygah in xeric environments are controlled by the erratic temporal and spatial occurrence of rains (Serventy

and Whittell, 1951; and pertinent discussion by Marshall, 1960). Moreover, extreme heat may cause widespread mortality in populations of Budgerygahs. In 1931, for instance, Australia experienced an exceptional heat wave, during which "millions" of Budgerygahs were found dead around water holes (Chisholm, 1958). Five tons of birds were said to have been removed from one dam, 30,000 dead birds were taken from another, and 60,000 from a third.

Like some other birds of xeric habitat in North America (Dawson, 1954), the Budgerygah becomes inactive during the middle hours of the day and seeks out a microclimate in which it can escape as far as possible from the intense solar radiation of this period of the day. Seth-Smith (1903) quotes Gould to the effect that during the heat of the day flocks of Budgerygahs sit so motionless among the leaves of the eucalyptus trees that they can be detected only with great difficulty.

In the ecology of its water relations, therefore, the Budgerygah has an adaptive pattern similar to that of the Mourning Dove (*Zenaidura macroura*) in the deserts of North America (Bartholomew and Dawson, 1954; Bartholomew and MacMillen, 1960), rather than the pattern of a small seedeater like the House Finch (*Carpodacus mexicanus*), which must drink repeatedly throughout the day in hot, dry environments (Bartholomew and Cade, 1956). In order to exploit the same kind of niche relationship with respect to sources of food and water as that of the Mourning Dove, the Budgerygah has had to evolve special abilities to withstand dehydration because of its smaller size (30 compared with 120 g) and because it cannot drink proportionately as much water in a single, short period as a dove can. Since the large numbers of Budgerygahs that use a given water hole could not possibly be supported by the food available in the immediate environs of the water, selection has doubtlessly favored a system of physiology that frees this small species from the necessity of drinking repeatedly throughout the day. Their resistance to dehydration allows Budgerygahs to exist in xeric environments by going to water no more than once or twice a day, so that they can spend the rest of their time searching for food in grasslands far away from the water hole.

From what is now known about the water economy of Budgerygahs, Savannah Sparrows (Cade and Bartholomew, 1959), and some other xerophilous passerines (D. S. Farner, orally; Cade, unpubl. data), the tentative hypothesis that desert-inhabiting birds have not evolved special physiological mechanisms for water conservation (Bartholomew and Dawson, 1953; Bartholomew and Cade, 1956) needs some modification. The information available as recently as a year ago led Chew (1961) to say that there possibly are no physiologically adapted desert species of birds

as there are of mammals. That statement may continue to apply widely to species of birds living in the relatively recent (Pliocene and Pleistocene) deserts of North America (see Cade and Bartholomew, 1959, for pertinent discussion). According to Udvardy (1958), half of the avian species occupying xeric (scrub) habitats in North America are but slightly modified populations derived from genera that include mainly forest or woodland inhabitants. Further, he points out that the North American scrub avifauna shows no phylogenetic affinity with the xerophil avifauna of the Palaearctic. If, as Udvardy suggests with some cogency, the Old World xerophil avifaunas have had a much longer history of development, and hence more opportunity for adaptive specialization to desertlike conditions, than the North American has had, then one might reasonably look for true desert birds, in the physiological sense, among these Old World xerophil groups. Our data on the Budgerygah are consistent with this expectation and prompt us to point out the desirability of obtaining information about the water economy of other Old World xerophilous psittacines and seedeaters such as the estrildinine and ploceinine finches, many of which are kept as cage birds and are, therefore, available for laboratory studies.

SUMMARY

The fact that Budgerygahs (*Melopsittacus undulatus*) exist in large numbers in arid, interior Australia suggests that this species may have special abilities to survive on a minimum intake of water. Moreover, aviculturists have long noted that domesticated Budgerygahs drink little by comparison with other small seedeaters such as finches.

Ten domesticated Budgerygahs were used to determine the following: (1) At air temperatures of 20 to 30° C and relative humidities of 18 to 40 per cent, Budgerygahs drink less than 10 per cent of their body weight per day, and some drink no more than 5 per cent per day; (2) When given saline water of 0.2 M or 0.3 M NaCl some Budgerygahs increase their drinking but tend to lose body weight, while others stop drinking but maintain body weight; (3) When deprived of all water, Budgerygahs can exist with little weight loss for at least 38 days at an average air temperature of 30° C and average relative humidity of about 30 per cent, and at 20° C some individuals can apparently survive indefinitely without water. Two birds were still in good health after 130 days without drinking. A 30-g

Budgerygah eats about four g of seeds per day with or without water to drink, although food consumption is somewhat greater at air temperatures around 20° C than at temperatures around 30° C. Budgerygahs lose about 0.65 g of water per day from their excreta, but respiratory water loss ranges from a low of about 44 mg per hour during complete rest or sleep to a high of 150 mg per hour during periods of moderate activity.

The calculated amount of water available to a Budgerygah in its food is 1.84 g per day, including free water and metabolic water. Of this total, about 1.19 g are available for respiratory water loss, since 0.65 g are lost in excrement. Experimental values for pulmocutaneous water loss indicate a minimum daily loss by this route of 1.86 g, possibly because the birds were excited by their confinement in the experimental apparatus. Since some body weight tends to be lost over a long priod of time without drinking, we feel that the true value for respiratory water loss lies somewhere between 1.86 and 1.19 g per day under basal metabolic conditions, probably near the lower value.

A nondrinking Budgerygah is able to maintain itself in water balance only by reducing activity as much as possible, for otherwise the increase in oxygen consumption coincident with activity would result in a net loss of water from the bird's tissues. The species appears to possess an intrinsically low basal metabolic rate, which may also be advantageous from the standpoint of water economy.

It is unlikely that wild Budgerygahs exist in arid environments for many days at a time without drinking. Probably they normally drink once or twice a day, like Mourning Doves in the deserts of North America. In order to exploit the same niche relationship with respect to sources of food and water as that of the dove, the Budgerygah has had to develop special abilities to withstand dehydration because of its smaller size and because it cannot drink proportionately as much water in a single draught as a dove can.

Recent information on several, diverse species of small, xerophilous birds indicates that some desert-inhabiting birds have developed physiological mechanisms for water conservation, as adaptations to their arid surroundings. It may be that such adaptations are more prevalent among species of the Old World xerophil avifaunas than among species inhabiting the recently developed deserts of North America, if it is true, as suggested by Udvardy, that the Old World groups have had a much longer history of association with arid environments.

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