

THE WATER ECONOMY OF LAND BIRDS*

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INTRODUCTION

TERRESTRIAL life is an aqueous phenomenon. Although the physiological and ecological roles of water are of paramount importance in the lives of all organisms, ornithologists have paid little attention to the water requirements of birds, except inferentially with regard to distribution and habitat preferences. It is an interesting commentary on the fads and fashions of science that prior to World War II many hundreds of papers had been published on the food habits of birds, but only a handful of papers had given even semi-quantitative attention to the no less important problems of water economy. The inevitable preoccupation of government biologists with possible economic importances, together with the relatively simple technique of stomach analysis, early led to many studies of food habits. In contrast, water economy, while of basic biological significance, has no obvious economic implications, and its analysis requires the labor of maintaining live birds under controlled or semi-controlled conditions.

During the past decade we have, together with various colleagues, undertaken a series of studies surveying the water economy of land birds in order to gain some preliminary insights into the ways different species have resolved the problem of maintaining a water balance. Although our studies have raised more questions than they have answered, they do allow the establishment of appropriate ecological and physiological perspectives. The purpose of this review is to sum up the conclusions from exploratory studies, in the hope that they may serve as a guide to more sophisticated physiological experiments and for more quantitative and precise ecological analyses. Our point of view is primarily ecological, and we shall confine our remarks to wild species of land birds. Readers interested in the domestic fowl should consult Sturkie (1954), and those requiring a broader physiological coverage should see Chew (1961).

Historical summary.—Fewer than a dozen publications bearing specifically on the water economy of wild birds appeared prior to 1950. Buxton (1923) broached the problem of the water relations of desert-inhabiting birds and mammals, and suggested that some species might depend upon metabolic water. Allen's (1925) semipopular treatment of avian biology contains a brief section on drinking habits, and Stresemann (1927) in his monumental treatment of birds for the *Handbuch der Zoologie* noted the general lack of information on avian water economy. Apparently as a

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result of Stresemann's brief summary, there was a flurry of interest in this field for a time before the war. For example, Gordon (1934) outlined a number of problems which are still current. Allard (1934) added a few pertinent observations, and Schildmacher (1936) reported on the survival times of several European finches when maintained on various salt solutions and dilutions of sea water.

In America, the pioneer quantitative and experimental works of Ken-deigh (1939; 1944) on evaporative water loss in the House Wren (*Troglodytes aedon*) and House Sparrow (*Passer domesticus*), and those of his student Seibert (1949) on water consumption of White-throated Sparrows (*Zonotrichia albicollis*), House Sparrows, and Slate-colored Juncos (*Junco hyemalis*), supplemented the more naturalistic studies of Vorhies (1928; 1945) on water deprivation of Gambel's Quail (*Lophortyx gambelii*) and Harlequin Quail (*Cyrtonyx montezumae*) and of Sumner (1935) and Stoddard (1931) on the use of succulent vegetation as a source of water by California Quail (*Lophortyx californicus*) and Bobwhite quail (*Colinus virginianus*), respectively. Although very astute inferences about the water relations of birds based on natural history observation have occasionally appeared in the literature (see, for example, Grinnell and Miller, 1944), we know of no other quantitative or experimental studies on the water economy of wild land birds prior to 1950.

Nature of the problem.—Our goal in investigating the water economy of birds is to gain an understanding of how birds obtain and utilize water in the diverse, and often extremely challenging, environments which they successfully occupy. Such an understanding can be attained only if birds are treated as integrated and functioning organisms adapted to their environments. It cannot be sought solely in terms of natural history, or of physiology, or of anatomy, or of behavior. The role of each of these aspects of the performance of the organism in the total pattern of its life must be assayed. From the standpoints of ecology and behavior it is important to find out how birds acquire water from the environment and how the natural conditions under which birds exist determine their needs for water. From the standpoints of physiology and anatomy, it is necessary to quantify the capacities and limitations of birds with respect to maintaining water balance under given environmental conditions. This quantification requires information on water-conserving mechanisms, rates of water exchange with the environment, systems of fluid transport, and mechanisms of osmoregulation and excretion.

To attempt to achieve a comprehensive grasp of a phenomenon which is central to the total biology of a complex organism like a bird may be an act of temerity in view of the limited amount of relevant data. The natural history and ecological literature on birds is, however, richer than

that for any other group of animals, and this information together with the knowledge about the biology of vertebrates allows a number of generalizations to be applied to birds by inference and analogy. Thus, it is possible to enumerate the major parameters of avian water economy.

Like other vertebrates, land birds have three main water sources: (1) free water in the form of streams, lakes, puddles, rain drops, snow, or dew, (2) preformed water contained in the food which they eat, and (3) oxidative or metabolic water produced incidental to their oxidation of organic compounds containing hydrogen. The sea and other saline waters can be considered as a potential water source, but their utilization by land birds requires unusual physiological capacities. The relative dependence of a given species of bird on each of these sources is a function of a variety of ecological and behavioral attributes among which general distribution, habitat preferences, food preferences, extent of home range, and daily and seasonal mobility may be mentioned. The water requirements of a given species will also be determined by such interrelated physical factors and physiological processes as (1) its rate of pulmocutaneous water loss, (2) the vapor tension and temperature of inspired and expired air, (3) its loss of water incidental to excretion, defecation, and thermoregulation, (4) its capacity for osmoregulation and electrolyte excretion, (5) its capacity for tolerating high blood viscosity and/or dehydration, (6) the salinity of the drinking water available, and (7) the salt and water content of the food.

WATER LOSS

It has long been known that in arid regions many small vertebrates, particularly lizards and rodents, are able to maintain dense populations in the complete absence of drinking water (Buxton, 1923). Following the pioneer studies of K. and B. Schmidt-Nielsen (1952 and preceding), it became apparent that some desert-adapted rodents can subsist with oxidative water as their only water source. This ability is related primarily to the minimal nature of the water losses of these rodents incidental to breathing, defecation, excretion, and insensible perspiration. It is obviously of interest to students of avian biology to know whether or not birds possess similar adaptations which will allow them to subsist without drinking.

Like all animals, birds produce water by their metabolism. Because of their high metabolic rates, the quantity of water thus produced by birds is greater in relation to body size than for other vertebrates. Moreover, from the standpoint of water conservation, birds have an important physiological advantage over mammals: their nitrogen excretion involves uric acid instead of urea. Molecule for molecule twice as much nitrogen can be excreted in uric acid as in urea. Furthermore, uric acid can be excreted in

a semi-solid suspension, whereas urea must be excreted in aqueous solution which, inevitably, involves a considerable loss of water. Most mammals require approximately 20 ml of water to excrete 320 mgm of urea, whereas a comparable amount of uric acid can be excreted in 0.5 to 1.0 ml of water. Even a kangaroo rat, *Dipodomys merriami*, which has an unusually efficient kidney, can excrete urea in a concentration only 20 to 30 times greater than that in its blood whereas birds can excrete uric acid in a concentration some 3,000 times greater than that in the blood (Smith, 1956: 23). As will be discussed later, however, the avian kidney is generally much less effective than the mammalian kidney in excreting electrolytes (Schmidt-Nielsen, 1960).

Evaporative water loss.—Despite the advantages of uricotelism, it has yet to be demonstrated that any normally active bird can satisfy its water requirements by oxidative water alone. This situation is explicable partly in terms of physiology and partly in terms of behavior. One of the behavioral factors implicated is the relatively rare occurrence among birds of adaptations for nocturnality and for fossorial life, habits which are characteristic of most small mammals and which minimize evaporative water loss (B. and K. Schmidt-Nielsen, 1950a). One of the physiological factors clearly implicated is the high rate of evaporative water loss characteristic of birds.

Bartholomew and Dawson (1953) measured the pulmocutaneous water loss of birds belonging to five orders and found that in the absence of temperature stress there is an inverse relationship between evaporative water loss and body weight. Subsequent studies by various workers have confirmed that this relationship is generally independent of taxonomic affinities and habitat (Figure 1). Presumably most of the evaporated water is lost from the respiratory system and air sacs and relatively little through the skin and plumage (see Salt and Zeuthen, 1960, for a thorough discussion of the structural and mechanical implications of the air sacs as a system for evaporative cooling). The source of this evaporative water loss has, however, not yet been compartmentalized.

Oxidative water.—A comparison of the amount of oxidative water produced with the amount of water lost through evaporation and other routes allows an estimate of the general importance of metabolic water in avian physiology. The maximum and minimum amounts of oxidative water which a bird of a given size will produce at rest can be calculated if the following assumptions are made: (1) the relation of body weight to basal metabolism is expressed by Brody's (1945) formula, kcal per day = 89 (wt. in kg)^{0.64}; (2) the oxidation of 1 g of fat yields 1.07 g of water and 9.2 kcal; (3) the oxidation of 1 g of carbohydrate yields 0.56 g of water and 4.10 kcal; (4) the oxidation of 1 g of protein yields 0.40 g of wa-

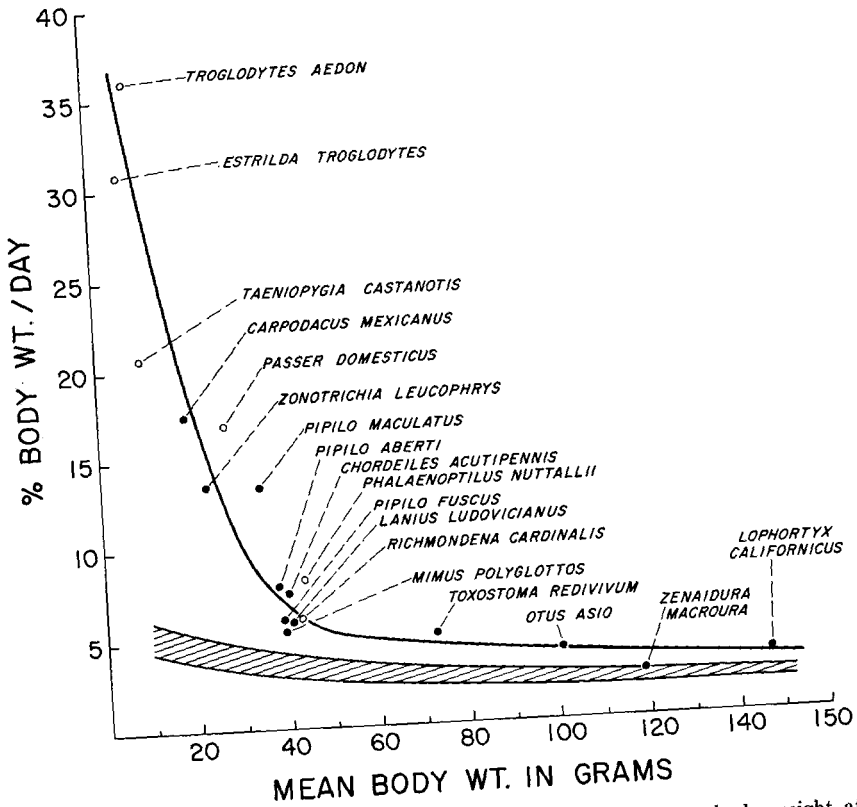


Figure 1. The relation of weight-relative evaporative water loss to body weight at ambient temperatures near 25°C. The cross-hatched curve indicates the theoretical relation between body weight and the production of metabolic water by birds in a basal condition utilizing exclusively carbohydrates (upper boundary), or exclusively proteins (lower boundary). The values for fats are intermediate. See text for basis of calculations. Data for birds indicated with solid circles are from Bartholomew and Dawson, 1953. The sources for the data on the birds shown by open circles are: *Troglodytes*, Kendeigh (1939); *Passer*, Kendeigh (1944); *Estrilda* and *Taeniopygia*, Cade (MS); *Phalaenoptilus*, Bartholomew, Hudson, and Howell (1962); and *Richmondena*, Dawson (1958).

ter and 4.10 kcal (Peters and Van Slyke, 1946: 7, 14). The theoretical curve for the production of oxidative water and the observed curve for evaporative water loss approximate each other most closely at body weights above 60 g and diverge sharply for most species at lesser body weights (Figure 1). If one assumes that large and small birds lose the same relative amounts of water in excretion and defecation, the gap between total water loss and metabolic production of water is relatively

greater for small birds than for large ones. Thus, even at moderate temperatures, the necessity for access to free water or the use of succulent food should be greater for small than for large birds, and for a bird weighing less than 50 g only a dramatic departure from the general pattern would allow it to place primary dependence on metabolic water.

Simultaneous measurements of evaporative water loss and metabolic rate have given specific confirmation of this generalization for three species. Cardinals (*Richmondena cardinalis*), with a mean body weight of 43 g, under basal conditions produce between 1.2 and 1.8 g of oxidative water per day, depending on the type of food metabolized, while they lose 2.4 g of water per day through evaporation (Dawson, 1958). The Cardinal thus loses 0.9 mg of water per ml of oxygen consumed—an extravagant figure when compared with the 0.5 to 0.59 mg of water per ml of oxygen lost by some heteromyid rodents (B. and K. Schmidt-Nielsen, 1950a). Even the xerophilous Zebra Finch (*Taeniopygia castanotis*) loses large relative amounts of water through respiration under normally hydrated conditions. These birds, which average slightly more than 11 g in weight, produce about 1.0 g of oxidative water per day (assuming an RQ of 1) in a resting state at room temperatures (20–25°C), while they lose about 2.1 g (about 20 per cent of body weight) per day through evaporation (Cade, Tobin, and Gold, MS). Thus, at best, the metabolic production of water compensates for only half of the evaporative loss, but even so the Zebra Finch seems to be considerably better off in this respect than the similar-sized House Wren (see Figure 1). A 40 g Poor-will (*Phalaenoptilus nuttallii*) in its thermal neutral zone at 35°C produces only about 0.5 g of oxidative water per day, but it loses 2.8 g per day through evaporation, and the ratio of water evaporated to oxygen consumed is 3.7 mg/ml (recalculated from Bartholomew, Hudson, and Howell, 1962, using assumptions presented above).

It is not known why small birds have a greater weight-relative evaporative water loss than large ones, but the greater loss of birds compared with mammals probably “. . . reflects a higher rate of respiratory loss owing to expiration of warmer air of greater moisture-carrying capacity than expired by rodents” (Dawson, 1958: 46).

Evaporative cooling.—The severity of water loss through evaporation under natural conditions is even more acute than indicated in Figure 1, because the ratio of water evaporated to oxygen consumed becomes increasingly more unfavorable the higher the environmental temperature. Birds, of course, depend upon the evaporation of water for the prevention of dangerously high body temperatures under conditions of heat stress (see Ecology and Evolution). For instance, in the Abert's and Brown towhees (*Pipilo aberti* and *P. fuscus*) evaporative water loss in-

creases four fold between 30° and 40°C, while oxygen consumption increases only slightly more than twice (Dawson, 1954). A similar situation exists in the Cardinal (Dawson, 1958), Poor-will (Bartholomew, Hudson, and Howell, 1962), and Zebra Finch (Cade, Tobin, and Gold, MS).

Survival without drinking.—Although it seems unlikely that any small bird under natural conditions can survive solely on the water produced by its metabolism, at least some individuals of three different species weighing less than 50 g are known to be capable of surviving without drinking for many days in captivity on a diet of dry seeds. Salt marsh Savannah Sparrows, *Passerculus sandwichensis* (Cade and Bartholomew, 1959), and domesticated stocks of two xerophilous Australian birds, the Budgerygah, *Melopsittacus undulatus* (Cade and Dybas, 1962), and the Zebra Finch (Cade, Tobin, and Gold, MS), possess such an ability. The first two species appear able to survive without drinking only by greatly reducing their level of activity (see Water Consumption), but the latter, when deprived of water, apparently can reduce its respiratory water loss per unit of oxygen consumed.

Field observations indicate that many species living in arid regions survive without visiting surface water at all or at least by doing so infrequently (Bates, 1933; Irwin, 1956). Although specific information is lacking, it is probable that these small species obtain sufficient water from their food, just as many of the larger predatory birds are known to do (see Water Deprivation). Some of these water-independent species, however, are seed-eaters, and these are the ones for which precise measurements of intake and outgo of water are badly needed.

From the preceding discussion, it is inviting to postulate that reliance on oxidative metabolism as the only source of water is a rare and perhaps nonexistent condition among small birds.

WATER CONSUMPTION

Another approach to understanding the water requirements of birds is to measure the quantities of water drunk by species adapted to widely divergent ecological conditions, maintained on a diet of known and limited water content. The fragmentary information on this subject reveals a relationship between size and *ad libitum* drinking in the absence of temperature stress. The existence of a generalized avian pattern is indicated by this relationship, and it also isolates some species whose performances are sufficiently atypical to suggest the existence of special adaptations which merit further and more detailed analysis.

As shown in Figure 2 and Table 1, *ad libitum* water consumption is inversely related to body weight, and the curve is strikingly similar to the comparable one for evaporative water loss. Thus, the data on water con-

sumption are consistent with the generalization that the high level of evaporative water loss in most small birds necessitates substantial intake of water by drinking or from succulent food. There are, however, some conspicuous departures from the general pattern of water consumption as related to size. The Budgerygah drinks far less than might be expected,

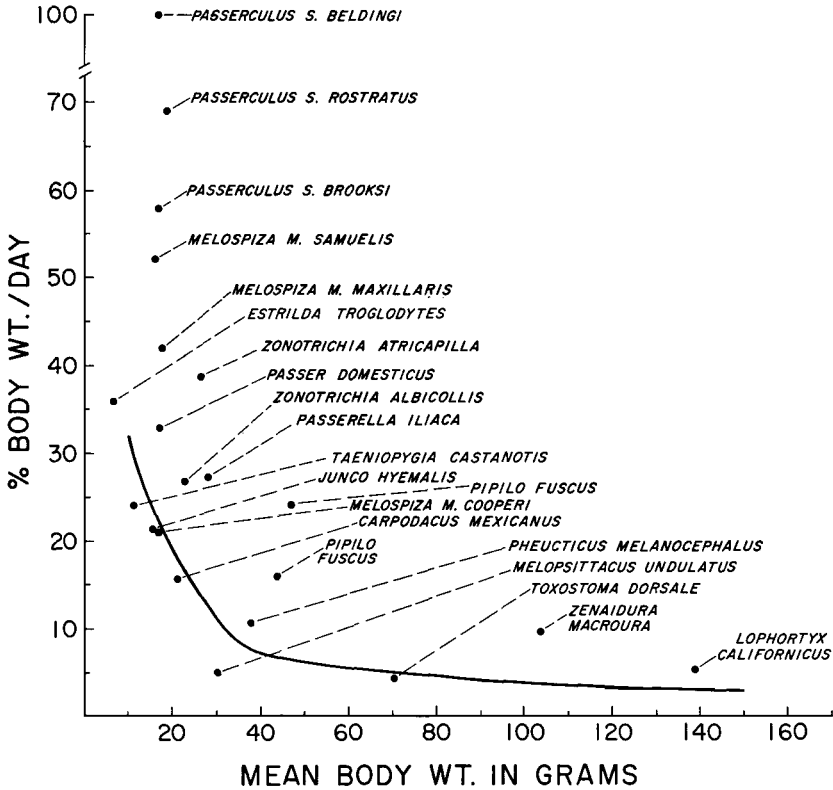


Figure 2. The weight-relative *ad libitum* water consumption of birds in the absence of temperature stress. See Table 1 for sources. The curve is for evaporative water loss and is the same as that in Figure 1.

and two subspecies each of the Savannah Sparrow (*P. s. beldingi* and *P. s. rostratus*) and the Song Sparrow (*M. m. maxillaris* and *M. m. samuelis*) drink far more. Interestingly, these exceptional species live in environmental situations where special problems of water availability exist. The Budgerygah occupies the arid interior of Australia, where rainfall is erratic and surface water, even when present, is often highly mineralized. The races of the Savannah Sparrow and Song Sparrow in question occupy salt marshes where the available water is highly saline, and consequently they face osmotic problems of some severity. Significantly, races of the

TABLE 1

SUMMARY OF DATA ON WATER CONSUMPTION OF TERRESTRIAL BIRDS IN THE ABSENCE OF TEMPERATURE STRESS

Species	Mean body weight (g)	Mean H ₂ O drunk % body wt./day		Source
		Ad lib- itum	Min.	
<i>Lophortyx californicus</i>	139.0	5.2	1.8	Bartholomew and MacMillen, 1961.
<i>Zenaidura macroura</i>	104.0	9.9	2.8	Bartholomew and MacMillen, 1960; MacMillen, 1962.
<i>Melospittacus undulatus</i>	30.0	5.0	<1.0	Cade and Dybas, 1962.
<i>Toxostoma dorsale</i>	70.0	4.4	—	Dawson and Bartholomew, MS.
<i>Passer domesticus</i>	17.3	32.9	—	Seibert, 1949.
<i>Taeniopygia castanotis</i>	11.5	24.4	<1.0	Cade, Tobin, and Gold, MS.
<i>Estrilda troglodytes</i>	6.5	35.7	—	Cade and Tobin, MS.
<i>Pheucticus melanocephalus</i>	37.0	10.3	—	Dawson and Bartholomew, MS.
<i>Carpodacus mexicanus</i>	20.6	16.0	10.0	Bartholomew and Cade, 1956; Poulson and Bartholomew, 1962b.
<i>Pipilo fuscus</i>	43.7	15.8	—	Dawson, 1954.
<i>Pipilo aberti</i>	46.8	23.5	—	Dawson, 1954.
<i>Passerculus sandwichensis brooksi</i>	17.5	58.2	—	Poulson and Bartholomew, 1962a.
<i>Passerculus s. beldingi</i>	17.0	100.0	45.9	Cade and Bartholomew, 1959; Poulson and Bartholomew, 1962a.
<i>Passerculus s. rostratus</i>	19.0	69.0	—	Cade and Bartholomew, 1959.
<i>Junco hyemalis</i>	15.8	21.4	—	Seibert, 1949.
<i>Zonotrichia atricapilla</i>	26.5	38.6	—	Cade, MS.
<i>Zonotrichia albicollis</i>	23.0	26.9	—	Seibert, 1949.
<i>Passerella iliaca</i>	28.0	26.8	—	Dawson and Bartholomew, MS.
<i>Melospiza melodia maxillaris</i>	18.2	41.8	—	Cade, MS.
<i>Melospiza m. samuelis</i>	16.4	52.5	—	Cade, MS.
<i>Melospiza m. cooperi</i>	16.8	21.1	—	Bartholomew and Cade, MS.

Savannah Sparrow and Song Sparrow which characteristically occupy freshwater marshes show an *ad libitum* water consumption which conforms closely to the expected values for birds of their weight.

It can be argued with considerable cogency that *ad libitum* drinking is a crude measure of the water needs of an animal. Some captive birds may drink merely because water is available and they have nothing else to do! The results from measurements of *ad libitum* drinking may be checked by approaching the problem in another way—namely, by determining the minimum daily ration of water required for maintenance of body weight. This second approach is time-consuming and has the disadvantage that most birds, when placed on a regimen of limited water, reduce their activity to levels far below normal. The method should be useful for compar-

tive purposes, but the values for minimum daily water requirements (Table 1) are still too fragmentary to support useful generalizations.

It is to be expected that water consumption, like evaporative water loss, will increase with increasing environmental temperature. This relationship has been examined in Mourning Doves (Bartholomew and Dawson, 1954), Brown and Abert's towhees (Dawson, 1954), House Finches, *Carpodacus mexicanus* (Bartholomew and Cade, 1956), and Budgerygahs (Cade and Dybas, 1962). In each of these species, except the Budgerygah, water consumption increases markedly at high temperatures. There can be little doubt that the increased water consumption offsets the loss of water incidental to an increase in heat dissipation by the evaporation of water from the respiratory tract.

WATER DEPRIVATION

A third way of surveying general aspects of the water economy of birds is to examine their tolerances to dehydration. This can be done most simply by maintaining the birds on a dry diet while depriving them of water and following their changes in body weight. Weight loss is not the most accurate index for degree of dehydration, because water deprivation sometimes reduces food consumption (see MacMillen, 1962). It does, however, closely parallel water loss, and for exploratory studies it is more convenient than measuring the tonicity or the viscosity of the serum or the plasma. For comparative purposes, data from animals denied water under controlled conditions of diet, temperature, and humidity are highly desirable. Such data are available for only a few birds, but these include a size range from 10 to 140 g and represent four orders. The data derived from studies of water denial are more variable than those on evaporative water loss or on water consumption, probably because a complex of physiological and behavioral factors is involved. For this reason, however, studies of dehydration may reveal capacities and adaptations with regard to avian water economy that measurements of the other more restricted parameters of the problem cannot.

Since evaporative loss and *ad libitum* consumption of water are both inversely related to body weight, large birds can be expected to lose weight less rapidly than small ones when denied water and maintained on a dry diet. Generally speaking this is probably so, although data on only three birds (California Quail, Mourning Dove, and House Finch) which fit the previously described generalization about the inverse relation of water consumption and evaporative water loss to body weight show this expected relationship. In these three, the loss per day of water deprivation is inversely related to body weight, as is the length of survival without water (Table 2).

There are, however, three species in which some individuals depart conspicuously from the "typical avian pattern" of water economy, and presumably more will be found as additional species are investigated. The Zebra Finch, which occurs widely in the arid parts of Australia, can get along in captivity on a diet of seeds without drinking (D. S. Farner, pers. comm.), but domesticated Zebra Finches can do so only after an initial period of weight loss and gradual adjustment to diminishing amounts of water over several days (Cade, Tobin, and Gold, MS). Most Savannah Sparrows lose weight and die in a few days if water is withheld, but some individuals from several subspecies are able to survive in captivity indefi-

TABLE 2
MEAN WEIGHT RESPONSES TO WATER DEPRIVATION OF BIRDS ON A DIET OF SEEDS WITH
A WATER CONTENT OF 9 TO 10 PER CENT

<i>Species</i>	<i>Initial weight</i>	<i>Per cent initial wt. lost/day</i>	<i>Per cent initial wt. at death</i>	<i>Source</i>
California Quail	139	1.6	50.2	Bartholomew and MacMillen, 1961.
Mourning Dove	105	4.8	63.3	Bartholomew and MacMillen, 1960.
House Finch	21	7.8	86.0	Bartholomew and Cade, 1956, 1958.

nitely on a dry diet without water. This capacity has not yet been studied in detail, but it is apparently associated with a marked reduction in activity (Cade and Bartholomew, 1959).

Some, but not all, domesticated Budgerygahs can survive indefinitely on a dry diet without drinking. The analysis of this capacity by Cade and Dybas (1962) indicates that the ability of this small, xerophilous Australian parrot to survive without drinking is related to (1) an unusually low basal metabolic rate for a bird of its size, which favors a low rate of evaporative water loss, (2) a profound reduction of activity under conditions of water deprivation, which further minimizes water loss, and (3) the capacity to produce extremely dry feces. It appears unlikely, however, that a normally active Budgerygah under natural conditions on a diet of grain could survive long without drinking; but the data on captives do indicate that the Budgerygah is better adapted to withstand dehydration than most other species of its size.

There are, of course, a number of species of primarily granivorous, or at least herbivorous, birds which live in areas where drinking water is rarely available. For relatively large birds such as quail, the small water requirements are easily met by eating succulent vegetation and insects.

California Quail in large, outdoor pens do not need water as long as green vegetation is available (Sumner, 1935), and when caged indoors will gain weight without drinking on a dry grain diet supplemented occasionally with either green plant material or insects (Bartholomew and MacMillen, 1960). A similar situation exists in Gambel's Quail (Vorhies, 1928; Gorsuch, 1934; Lowe, 1955; Gullion, 1960), and Harlequin Quail (Leopold and McCabe, 1957), and these species often occur many miles away from surface water. Even the small House Finch, which dies in three or four days on a dry diet without water, will thrive indefinitely and at a normal level of activity if given supplementary apple, celery, or lettuce (Bartholomew and Cade, 1956). At present there is no convincing evidence contrary to the assumption that small, primarily granivorous birds such as various desert-inhabiting fringillids must, in the absence of drinking water, supplement their dry seed diet with succulent plant or animal foods. However, the degree to which such forms are dependent upon succulent foods and sources of drinking water varies greatly from species to species, ranging from typically water-dependent forms such as the House Finch to xerophiles such as the Zebra Finch, which can survive for days on a diet containing 10 per cent moisture or less. Irwin's (1956) interesting field observations on the drinking habits of birds in the Kalahari Desert and adjacent parts of Bechuanaland indicate that a systematic study of the water economies of the fringillids and ploceids living in those regions would be most profitable in elucidating evolutionary trends toward independence of sources of free water. Some species are restricted to the immediate environs of the water holes, other closely related forms visit water only once or twice a day, and still others apparently seldom or never come to the holes for a drink.

Insectivorous birds such as the Verdin (*Auriparus flaviceps*) and the Rock Wren (*Salpinctes obsoletus*) probably obtain all the water they need from the body fluids of the insects they eat. It is interesting that most of the passerine birds which show primary affinity for the desert scrub habitat in California (Miller, 1951) are insectivorous. Indirect evidence for the importance of insects as a water source is available. For example, Irwin (1956) saw no species of the following passerine families at water holes in the arid regions of Bechuanaland: Timaliidae, Muscicapidae, Turdidae, Sylviidae, Zosteropidae, Prionopidae, Dicruridae, Paridae, Laniidae, and Nectariniidae. Significantly, these families all consist primarily of insectivorous forms. The swallows are a notable exception among insectivorous passerines in that they show a strong attraction to surface water and drink frequently. It is tempting to postulate that these fast-flying aerial feeders, because of their great expenditure of energy in flying, lose more water by evaporation than do their less energetic coun-

terparts on the ground. Thus, they may drink to make up this deficit (see Salt and Zeuthen, 1960, for a discussion of evaporative water loss during intense flight).

The larger predatory birds obtain adequate quantities of water from their food under most circumstances. Schildmacher (1936) kept a Tawny Owl (*Strix aluco*) for many months without water. Cade (unpublished data) has found that the following species can maintain or even gain weight in captivity on a diet of flesh with no drinking water: Gyrfalcon (*Falco rusticolus*), Peregrine Falcon (*F. peregrinus*), Prairie Falcon (*F. mexicanus*), Merlin (*F. columbarius*), Kestrel (*F. tinnunculus*), Sparrow Hawk (*F. sparverius*), Sharp-shinned Hawk (*Accipiter striatus*), Cooper's Hawk (*A. cooperii*), Goshawk (*A. gentilis*), Red-tailed Hawk (*Buteo jamaicensis*), Rough-legged Hawk (*B. lagopus*), Snowy Owl (*Nyctea scandiaca*), Great Horned Owl (*Bubo virginianus*), Hawk Owl (*Surnia ulula*), Boreal Owl (*Aegolius funereus*), Screech Owl (*Otus asio*), Northern Shrike (*Lanius excubitor*), and the Loggerhead Shrike (*L. ludovicianus*). Most of the species listed above drink occasionally when water is available, but drinking water is not necessary for them to maintain water balance under moderate conditions. This conclusion is probably generally applicable to flesh-eaters.

Bartholomew and Cade (1957) found that Sparrow Hawks, when kept without water in an ambient temperature of 40°C for 48 hours, maintained body weight on beef heart alone, even though they panted almost continuously. Some raptors, such as the Peregrine Falcon (*Falco peregrinus babylonicus*) of the Middle East, or "red-naped shaheen," and the Sooty Falcon (*Falco concolor*) of North Africa exist and breed under the harshest desert conditions known. Booth (1961) found the latter breeding in August on a vast stretch of the Libyan Desert devoid of all vegetation. The birds had their clutch in a cairn of rocks marking a camel trail. The temperature in the shade under the cairn was 108°F on 26 August, and temperatures of 120°F are not uncommon in the area in July. The adults were feeding at dawn and dusk on the autumn migrants crossing the desert. The "red-naped shaheen" similarly feeds on bats at dusk (Dementiev, 1951). During the heat of the day, raptors and other large birds often soar at altitudes where the air temperature may be 10° to 15°C cooler than at ground level (Salt and Zeuthen, 1960). On the basis of the above data, we suggest that the larger carnivorous birds, by appropriate modifications of their activity patterns, are able to survive without drinking water even in regions of extreme heat and aridity, although they will, to be sure, visit water where available.

Moist food appears to be the only source of water for nestlings of all avian species (see Gordon, 1934), except for certain doves and sandgrouse

(*Pterocles* spp.) that apparently drink water and regurgitate it to the young (see the interesting translation from a Russian source on page 403 of Salt and Zeuthen, 1960). It would be interesting to know how much water is used by the adults of certain cardueline finches, such as the redpolls (*Acanthis*), which feed their young seeds and other vegetable materials that are first moistened in their crops.

THE USE OF SALT WATER

The role of salt water in the water economy of birds has long intrigued ornithologists, but until recently only random natural history observations and inferences drawn from distributional data have been available. The recent discovery by Schmidt-Nielsen and associates (1958, 1960) of extra-renal salt excretion in several orders of aquatic birds has, however, opened up an entirely new area of physiological research. In the present review, we focus attention only on the salt metabolism of land birds, none of which has yet been demonstrated to have extra-renal mechanisms for electrolyte excretion.

A consideration of electrolyte metabolism is of particular interest in a survey of the water economy of land birds. On the one hand, it offers a powerful aid to understanding the mechanisms of renal function, and, on the other, it can contribute to an understanding of the ecology of desert birds which have access to saline springs, temporary pools in alkaline pans, or the sea as possible sources of drinking water, as well as the ecology of those birds which live on waterless oceanic islands or in coastal salt marshes.

Aside from the early work by Schildmacher (1936) on the effects of various salt solutions and dilutions of sea water on the survival of several species of European finches and scattered natural history references to the eating of salt by wild birds (see Van Tyne and Berger, 1959: 258), the role of saline water in the biology of wild land birds has received attention only in the last five years. Consequently, there is so far little basis for either physiological or ecological generalization.

The ocean contains slightly more than 3 per cent salt, while the body fluids of birds and other terrestrial vertebrates contain about 1 per cent. Because of this difference, the sea is a very difficult source from which to obtain physiologically usable water. If a bird drinks sea water, the fact that its body fluids are less concentrated than the ingested fluid results in water moving osmotically from the body to the gut, and it also results in an influx of salt into the body fluids. Thus, for a bird to obtain physiologically usable water from the sea or other highly saline water, it must do osmotic work to shift the water from its gut into its fluids, and it must also have an excretory system capable of retaining this water while ex-

creting the excess salt which is taken in. The kidneys of most birds that have been examined generally have less concentrating ability than those of mammals, perhaps because many birds lack the loop of Henle which apparently acts as a counter-current multiplier system (see reviews by Schmidt-Nielsen, 1958, and Sperber, 1960). In association with this relatively poor renal capacity, marine birds have evolved an extra-renal excretory organ, the salt gland, which is homologous with the nasal gland of terrestrial forms. This salt gland can secrete a solution of NaCl more concentrated than sea water and hence allows marine birds to use the sea as a source of water (Schmidt-Nielsen, 1960).

As far as is known at present, no terrestrial bird has a functional salt gland or any other extra-renal site of salt excretion, but certain suggestive facts about members of the Motacillidae should be mentioned in passing. Wagtails (*Motacilla* spp.) have nasal glands which are relatively larger than those of other land birds examined, and which approach in relative size the functional salt-excreting glands of some aquatic forms (Technau, 1936; Portmann, 1950). In Bechuanaland some populations of the pipit *Anthus novaeseelandiae* are closely associated with saline pans and apparently drink salt water (Irwin, 1956), and Rock Pipits (*A. spinoletta*) migrating along the coasts of the British Isles feed to a considerable extent on marine invertebrates of the intertidal zone (Gibb, 1956).

Most, if not all, land birds must rely on their kidneys for salt excretion. It is to be expected, therefore, that most land birds will be unable to drink sea water or to use water from saline springs or lakes with a salt concentration more than about 1 per cent. To date, data on the ability to process salt water are available only for the Rock Dove, *Columba livia* (Scotthorne, 1959), and for the terrestrial species and subspecies shown in Table 3, and of these only two, the Savannah Sparrow and Zebra Finch, appear capable of using the sea for drinking. Some birds which do not require much water, like the Budgerygah and the salt marsh Savannah Sparrow (*P. s. rostratus*), will undergo voluntary deprivation or reduction in drinking rather than drink concentrated salt solutions, so the figures available for such species probably do not represent values comparable to those obtained for other species.

Patterns of ad libitum drinking.—The weight-relative volumes of saline water drunk by different species of birds vary widely and suggest the existence of at least three major patterns of response that may have both physiological and ecological significance.

Pattern A. In the House Finch, in the races of Savannah Sparrows and Song Sparrows (*Melospiza melodia*) that inhabit freshwater marshes, and in the Mourning Dove, the quantity of fluid drunk increases directly and dramatically with increasing salinity (Figure 3). Individual birds may

ingest more than their body weight of salt water daily. At some critical concentration, which is 0.25 M NaCl for the Mourning Dove and 0.5 M NaCl for the House Finch, drinking falls off sharply, and some individuals may refuse to drink even though experiencing severe weight loss. The increase of water consumption with increase in salinity of the drinking

TABLE 3
CAPACITY OF TERRESTRIAL BIRDS TO USE SALT SOLUTIONS AS DRINKING WATER¹

Species	Maximum salinity for weight maintenance		Source
	Per cent sea water	Molarity NaCl	
<i>Lophortyx californicus</i>	40	—	Bartholomew and MacMillen, 1961.
<i>Zenaidura macroura</i>	25	0.15	Bartholomew and MacMillen, 1960.
<i>Melospittacus undulatus</i>	—	0.30	Cade and Dybas, 1962.
<i>Taeniopygia castanotis</i>	—	0.60	Oksche, Farner, Serventy, Wolff, and Nicholls, 1963.
<i>Carpodacus mexicanus</i>	—	0.25	Bartholomew and Cade, 1958.
<i>Passerculus sandwichensis brooksi</i>	—	0.30	Poulson and Bartholomew, 1962a.
<i>Passerculus s. beldingi</i>	100	0.60	Poulson and Bartholomew, 1962a; Cade and Bartholo- mew, 1959.
<i>Passerculus s. rostratus</i>	100	0.55	Cade and Bartholomew, 1959.
<i>Passerculus sandwichensis</i> ²	75	0.40	Cade and Bartholomew, 1959.
<i>Zonotrichia leucophrys gambelii</i>	—	0.20-0.30	Oksche, Farner, Serventy, Wolff, and Nicholls, 1963.
<i>Zonotrichia atricapilla</i>	50	—	Cade, MS.
<i>Melospiza melodia maxillaris</i>	50	—	Cade, MS.
<i>Melospiza m. samuelis</i>	50	—	Cade, MS.
<i>Melospiza m. cooperi</i>	—	0.40	Bartholomew and Cade, MS.

¹ The pioneer measurements of Schildmacher (1936) are not included because his methods of measurement are not compatible with those used here.

² Mixed sample of *brooksi*, *nevadensis*, and *anthinus*.

solution is consistent with a familiar theory of the thirst mechanism in vertebrates: the ingestion of salt increases the tonicity of the body fluids, and this hypertonicity stimulates an osmoreceptor which evokes a drinking response. This feed-back system remains adequate for maintaining a water balance when the drinking water is not highly saline, but at high molarities the bird can extract progressively smaller quantities of water from the fluid it drinks, and eventually—despite a voluminous fluid ingestion—it loses weight about as fast as if it were not drinking at all.

Pattern B. This pattern is found in the California Quail (Bartholomew and MacMillen, 1961). The volume of ingested fluid is about as expected on the basis of body weight and remains unchanged with increases in

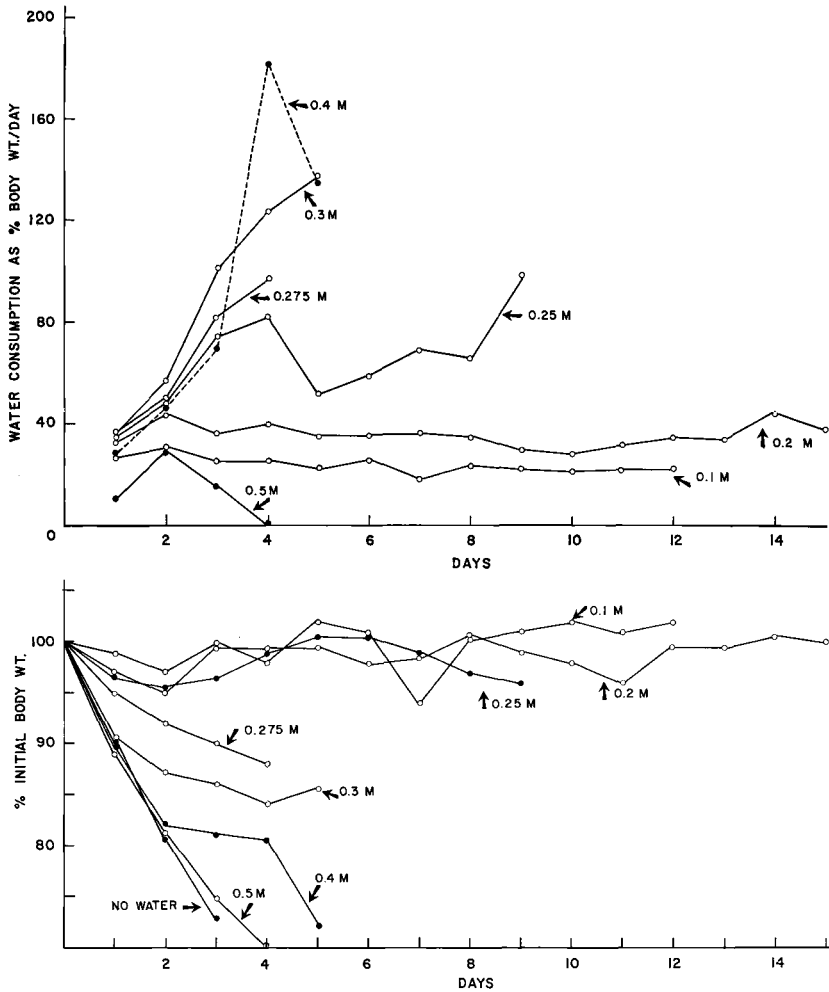


Figure 3. Mean *ad libitum* drinking of various solutions of NaCl by House Finches and its effect on body weight (from Bartholomew and Cade, 1958).

salinity, even though at the higher concentrations the birds lose weight more rapidly than they would if not drinking at all. In this species the drinking response does not fit the same simple feed-back model used to explain pattern A. The Budgerigah has a somewhat similar pattern, although, when drinking saline water, individual birds vary greatly in the amounts they take (Cade and Dybas, 1962).

Pattern C. A third pattern is found in two races of Savannah Sparrow which breed in salt marshes in western North America, *P. s. beldingi* and

P. s. rostratus. In captivity these sparrows have an unusually high consumption of distilled water, and their drinking of salt water either decreases or remains nearly constant with increasing salinity (Cade and Bartholomew, 1959; Poulson and Bartholomew, 1962a). Individuals of *beldingi* have a very high drinking rate (84 to 112 per cent of body weight per day) on distilled water and on concentrations up to 0.6 M NaCl; on 0.7 M NaCl their drinking is reduced to about 75 per cent of body weight per day. Salt marsh races of the Song Sparrow (*M. m. maxillaris* and *M. m. samuelis*) in the San Francisco Bay region of California have a similar pattern, but their consumption of distilled water is not quite so high, nor can they maintain weight on full-strength sea water (Cade, MS). It is of interest that the water of San Francisco Bay is much less saline than the open sea.

Salinity discrimination.—There are probably many factors which contribute to these three distinctive patterns of *ad libitum* consumption of salt water. Taste, one of the most obvious and testable of these, is particularly relevant since it is well known that granivorous birds often seek out natural sources of salt (Van Tyne and Berger, 1959: 258). However, almost no quantitative data are available on the sense of taste in land birds. Duncan (1960) has pointed out that taste buds are much less numerous in those birds that have been examined than in mammals and has suggested that the sense of taste in birds may, therefore, be relatively unimportant. The ability of four species of wild land birds to discriminate between various salinities has been tested in choice experiments. The House Finch shows no preference for distilled water over solutions of NaCl of 0.15 M or less, but drinks more than twice as much distilled water as 0.2 M NaCl when both are available (Bartholomew and Cade, 1958). Mourning Doves do not discriminate between distilled water and 12.5 per cent sea water or between 12.5 and 25 per cent sea water, but they prefer 25 per cent to 37.5 per cent, and 37.5 to 50 per cent sea water (Bartholomew and MacMillen, 1960). The California Quail shows no preference for distilled water as compared with 12.5 and 25 per cent sea water, but it chooses 25 per cent sea water in preference to 37.5 per cent. This quail will undergo short periods of deprivation rather than drink 37.5 per cent sea water, but if individuals become dehydrated, they will drink even 70 per cent sea water (Bartholomew and MacMillen, 1961). When members of two subspecies of Savannah Sparrow were given equal access to distilled water and 0.25 M NaCl, both drank more distilled water than salt water; however, the ratio of distilled water to salt water drunk was such that the weight-relative salt ingestion of the salt marsh form, *P. s. beldingi*, was about three and a half times that of *P. s. brooksi*, which breeds in freshwater marshes (Poulson and Bartholomew, 1962a).

From these findings it appears likely, first, that these species can and do distinguish between salt concentrations; second, that if given the choice they will drink solutions the concentrations of which they can readily tolerate; and third, that at least one form, *P. s. beldingi*, prefers a higher weight-relative salt ingestion than do the others. We therefore suggest that the three patterns of salt water consumption outlined above

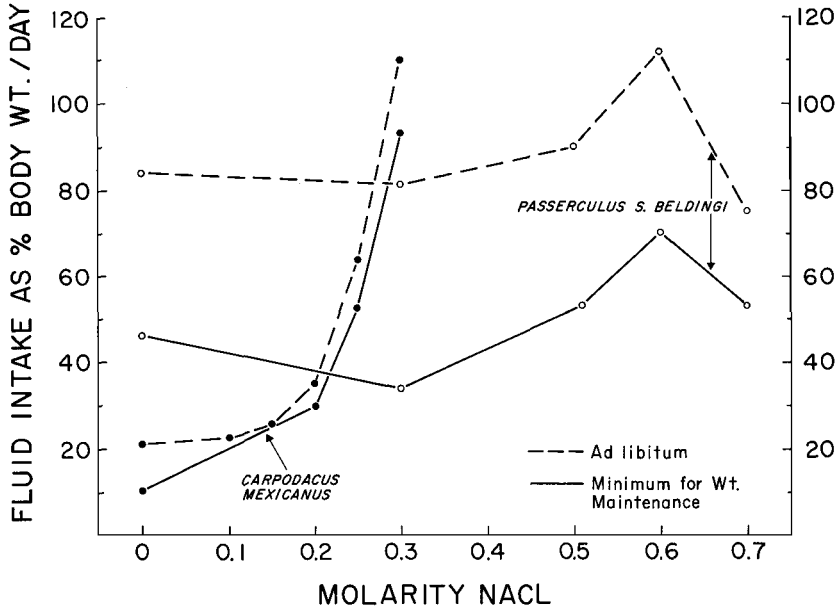


Figure 4. The relation of *ad libitum* drinking and the minimum fluid ingestion required for weight maintenance to molarity of drinking solution in *C. mexicanus* and *P. s. beldingi*.

are based not just on taste preference but are related to basic mechanisms of water and electrolyte balance. Further investigation will require methods of measurement more refined than those so far discussed (see Electrolytes in Blood and Urine).

Minimum daily ration.—The problem of relating intake of saline water to salt balance and kidney function can be approached profitably from another direction by a simple method which minimizes the problems associated with choice. This method is the determination of the relation of salinity to the minimum daily fluid ration on which birds can maintain their weight. Such data are available only for the House Finch and the Savannah Sparrow (Poulson and Bartholomew, 1962a, 1962b). From Figure 4 it is apparent that the minimum adequate daily ration for the House Finch increases regularly with increasing salinity, but is always

less than the level of *ad libitum* drinking. Thus, at high molarities more fluid must be processed by this species per amount of physiologically usable water obtained than at low molarities. In *P. s. beldingi*, as in the House Finch, minimum adequate daily ration parallels *ad libitum* drinking in a striking manner. These Savannah Sparrows can, however, maintain weight on a smaller ration of 0.3 M NaCl than of either distilled water or of solutions more concentrated than 0.3 M. Both species reduce activity significantly when drinking salt water that is near their limits of tolerance. These results not only emphasize that important differences exist among fringillids, but they also show that *ad libitum* drinking, even under the highly artificial conditions of confinement in small cages, is correlated with physiological needs.

On the basis of (1) ability to discriminate between different salt solutions, (2) a willingness to drink any solution (under duress) from which physiologically usable water can be obtained, and (3) from the fact that *ad libitum* drinking and minimum water ration show the same general dependence on salinity, it is reasonable to conclude that the observed differences in the intake of saline solutions in different species are related to physiological differences. These differences can best be considered at a level of integration other than that of the whole organism—namely, by an analysis of some aspects of kidney function.

ELECTROLYTES IN BLOOD AND URINE

One of the most obvious ways to gain insight into the comparative physiology of the avian kidney is to measure the freezing point depressions and chloride concentrations of the plasma and urine of different species under various conditions of salt ingestion. This should indicate (1) ability to tolerate variations in the osmotic concentrations of the body fluids, (2) the relation between drinking, salt intake, and osmotic concentration of body fluids, (3) the relation of salt intake to salt output, and (4) the ability of the kidney to concentrate electrolytes.

Relevant and comparable data on these topics are available only for the House Finch and two subspecies of Savannah Sparrow (Poulson and Bartholomew, 1962a, 1962b). Even these limited data are instructive, because these species show two of the more divergent patterns of water economy so far found in passerines.

The kidney contributes to the regulation of the total osmotic concentration of the body fluids and also to the relative concentrations of the various ions in the body fluids by controlling the volume of water and the concentrations of ions entering the urine. The blood plasma is a convenient sample of the body fluids, and the clear liquid which is voided with the uric acid and fecal materials can be treated as a sample of the urine.

By suitable microchemical methods the osmotic pressures and chloride concentrations in the plasma and urine can be compared. As long as the kidney is doing its job, the freezing point depression (a convenient measure of total osmotic concentration) and chloride concentration of the plasma should remain uniform and independent of the amount of salt ingested, while these quantities in the urine should vary with the amount of ingested salt. In the two species under consideration, both osmotic

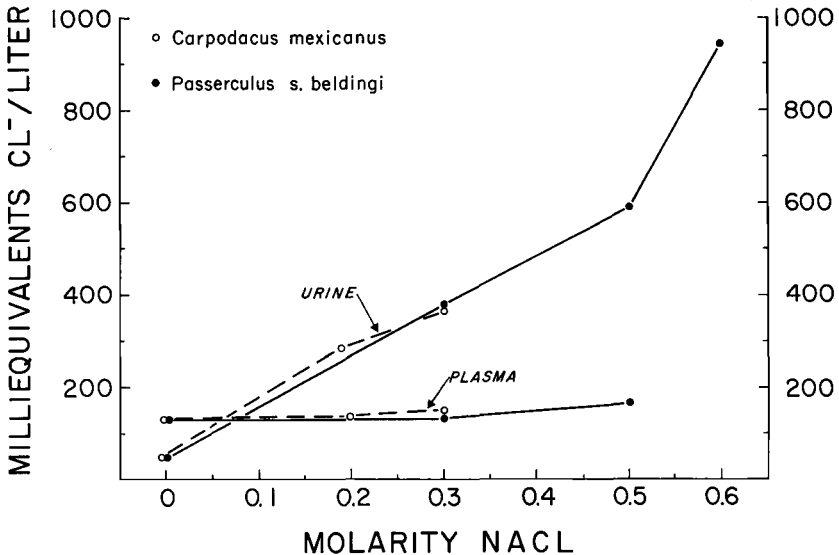


Figure 5. The relation of chloride in urine and plasma to molarity of drinking solution.

pressure and chloride concentration show similar responses to salt ingestion, so for simplicity we shall confine consideration to the latter. The relation of chloride concentrations in blood and urine to intake of NaCl in birds drinking salt solutions *ad libitum* is shown in Figures 5 and 6. In both species the amount of chloride in the urine increases directly with the salinity of the drinking solution. At molarities below 0.2 the chloride in the plasma remains unchanged. At molarities of 0.3 and greater, plasma chloride increases; the *beldingi* race of the Savannah Sparrow can tolerate this increase, but the House Finch cannot. The capacity of the kidney to excrete excess salt can be estimated from the ratio between chloride concentrations in the urine and in the plasma during periods of large salt intake. The House Finch cannot elevate the chloride level in the urine more than 2.4 times that in its plasma, but *Passerculus sandwichensis beldingi* can produce urine with a chloride concentration approximately 5

times that of its plasma (Figure 6). *P. s. brooksi* is intermediate with a ratio of 3.3.

In summary, the ability of *P. s. beldingi* to obtain water from highly saline sources, and the inability of *C. mexicanus* and *P. s. brooksi* to do so, is explicable in part by the former's tolerance of higher levels of

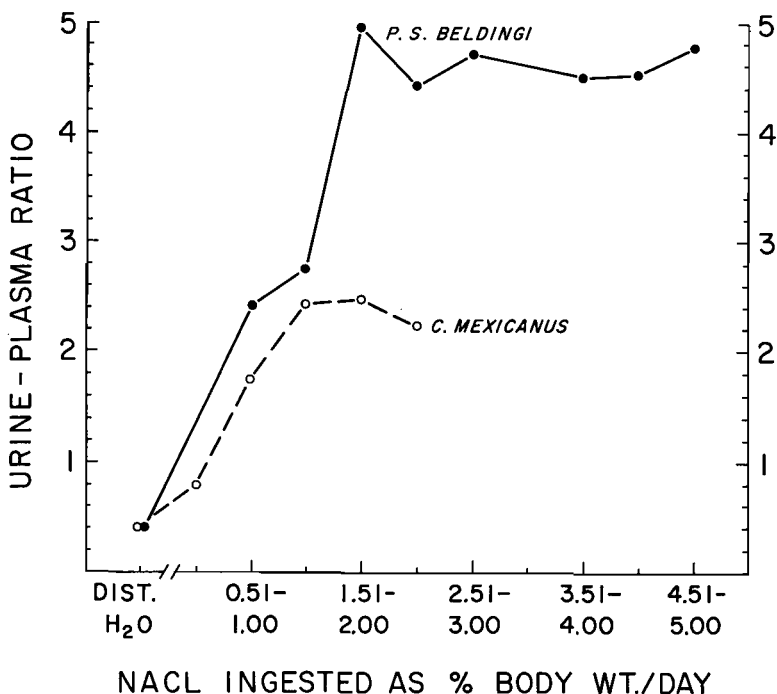


Figure 6. The relation of urine-plasma chloride ratios to ingestion of NaCl during *ad libitum* drinking.

chloride and other osmotically active particles in the blood, and in part by its ability to excrete unusually high levels of chloride in its urine.

The methods so far employed for obtaining urine samples from small birds do not allow differentiation between the contributions to the process of urine concentration in the kidney and possible resorption of water by the lower gut or cloaca. Whatever the mechanism, it is of interest that the maximum chloride concentration in the urine of *P. s. beldingi*, 960 mEq/L, is as great as that reported for the nasal secretion of Leach's Petrel (*Oceanodroma leucorhoa*), which produces the most concentrated salt gland secretion known (Schmidt-Nielsen, 1960). Furthermore, the ability of *beldingi* to concentrate chloride compares favorably with that of some mammals.

ECOLOGY AND EVOLUTION

From the information reviewed above it is apparent that the data are insufficient to allow more than a definition of the parameters of the problems of water economy in land birds and to furnish some rough quantitative estimates of the physiological capacities of birds of several orders and various ecological types with respect to water consumption, water loss, and the processing of saline solutions. The available information does, however, allow us to suggest some physiological limits within which the behavior of most birds must be accommodated if they are to meet successfully the challenges of their particular niches in the physical and biotic environments.

Most land birds are completely dependent upon fresh drinking water or succulent foods to supply their physiological needs for water. Although the full significance of the curves for weight-relative evaporative water loss (Figure 1) and water consumption (Figure 2) is still to be learned, it seems likely that these curves describe the general pattern of avian water economy. Since most land birds occur in mesic and humid environments where water and succulent foods are abundant, the high rate of turnover of water which characterizes small birds places most of them at no particular disadvantage.

Arid environments.—Although the present data indicate that departures from the general pattern of avian water economy are rare, there is evidence that a few species have become adaptively specialized to niches which place unusually severe demands upon their water economy. Small seed-eating birds which occupy waterless tracts of desert, waterless oceanic islands, or coastal salt marshes exist in situations posing acute difficulties in obtaining adequate amounts of water. It is, therefore, not surprising that birds occupying these situations deviate from the general pattern and show unusual capacities with respect to tolerance of dehydration and kidney function.

The ecological aspects of avian water economy are thrown into sharpest relief under extreme desert conditions. Except for goatsuckers, owls, and one or two species of parrots, desert birds are primarily diurnal. Thus, unlike small desert mammals, birds are exposed to desert conditions at their most extreme. They must cope with high air temperatures and intense solar radiation, as well as with a scarcity of water. Not only do they respire air of low humidity, but unlike most small mammals, they are frequently faced with the necessity for extensive evaporative cooling. In addition, few birds are fossorial, and thus they cannot minimize their evaporative water loss by building up the humidity within burrows, nor can they escape the heat by going underground. Furthermore, the small size of many species and their high weight-relative metabolism make it

impossible for them to avoid an extensive turnover of materials, including water, which are often in short supply.

It is of interest that summer dormancy (aestivation) has not yet been demonstrated in birds, although it is of course well known in mammals which live in areas of seasonal drought, particularly ground squirrels (see Bartholomew and Hudson, 1960). The combination of diurnal habits (presumably a function of the primary dependence of most birds on acute vision for finding food), and the lack of burrow-dwelling and summer dormancy, pose for birds a particularly demanding series of adjustments, if they are to occupy arid lands successfully. The difficulty of the problems facing birds is indicated by the fact that in the deserts of the Holarctic Region, the resident populations of mammals are many times as great as the resident populations of birds. (Australian deserts appear to represent a special situation in this regard and will be discussed later.)

Despite the fact that the fundamental patterns of avian biology place birds at a disadvantage in deserts, they do have several physiological and behavioral characteristics which stand them in good stead. The most obvious of these is their impressive mobility, which allows many species to seek out remote and isolated water supplies (see Bowen, 1927; Bates, 1933; Cameron, 1938). Other favorable attributes are their high level of resting body temperature (39° – 42° C for most birds) and their capacity to tolerate elevated body temperatures as high as 45° C for several hours at a time (Bartholomew and Dawson, 1958). High body temperature allows the establishment and maintenance of a favorable physical relationship for heat transfer from body to environment even at high ambient temperatures.

Thermoregulation.—The fact that birds store heat in hot environments, and consequently undergo a rise in body temperature, results mainly from the inability of their panting to produce adequate evaporative cooling (Kendeigh, 1944; Wallgren, 1954; Dawson, 1954, 1958). At high ambient temperatures birds from the size of *Troglodytes aedon* to that of *Columba livia* can ordinarily lose no more than 40 to 50 per cent of their resting heat production through evaporation (see review by King and Farner, 1961). Consequently, small birds must necessarily be able to tolerate elevated body temperatures when the temperature of the environment approaches that of the body. In fact, so far as is known, the only bird which can maintain body temperature below air temperature by evaporation of water from its gular and respiratory tract is the Poor-will, which not only has an unusually low level of metabolic heat production but which also accelerates evaporation by a rapid fluttering of its extensive gular area when subjected to heat stress (Bartholomew, Hudson, and Howell, 1962). A similar situation probably exists in other goatsuckers

(Cowles and Dawson, 1951; Lasiewski and Dawson, MS). Salt and Zeuthen (1960) have made calculations suggesting that it might be possible for a sandgrouse to evaporate an amount of water equal to three or four times the basal metabolism; if so, this bird would be able to hold its body temperature below ambient by evaporative cooling. Certainly the remarkable intake of water by sandgrouse merits physiological investigation from this point of view.

Since normally active birds lose more water by evaporation than they produce by metabolism, and since evaporative cooling is usually inadequate to dissipate the heat of metabolism at temperatures above the thermoneutral zone, if a granivorous bird, such as the Mourning Dove, is to occupy desert regions, it has to depend on the availability of surface water. The time that can elapse between visits to water by such a bird will be a function of environmental temperature and humidity, level of activity, ability to tolerate dehydration and elevated body temperature, and capacity to take in water.

The water problems of land birds are particularly acute during the breeding season. The female must process more water than normal for egg production, and the nestlings of most species must necessarily depend on succulent food for their source of water. In the case of doves, the water needs of both male and female are increased incidental to the production of pigeon milk, and the same must be true of those granivorous species which moisten the seeds in their crop before feeding them to the young. It is not surprising, therefore, that in arid areas the breeding season is closely correlated with the availability of water or with the appearance of succulent vegetation. In winter-rainfall deserts, the birds tend to breed in late winter or early spring. In summer-rainfall deserts, breeding is usually later (see Miller, 1960, for a cogent discussion). In areas, such as much of inland Australia or parts of Africa, with mild winters and erratic rainfall, breeding may take place at any season depending on the occurrence of local rains (Keast and Marshall, 1954; Marshall and Disney, 1957; Marshall, 1961).

Evolutionary considerations.—Detailed information on the ecological aspects of water economy in desert birds is scanty, but several patterns of adaptation can be discerned. Before examining these patterns, however, a consideration of factors affecting their evolution is important, because adaptation cannot validly be treated, except in a purely descriptive sense, unless change with time is taken into account. We shall attempt, therefore, to fit our ecological discussion into an appropriate evolutionary context.

The basic biological attributes of birds are such that species which do not have restrictive habitat requirements can sometimes successfully oc-

cupy deserts even though they lack special physiological adaptations related to water. The House Finch is a good example (Bartholomew and Cade, 1956; Salt, 1952). Its rate of evaporative water loss is several times its rate of oxidative water production. Even in the absence of heat stress it can survive on a dry diet for only three days without drinking. It has limited ability to obtain physiologically usable water from solutions more saline than its own body fluids. Its *ad libitum* water consumption is more than 20 per cent of body weight per day, and it cannot maintain weight unless given drinking water equal to a little less than 10 per cent of body weight per day. Even so, the House Finch is numerically one of the most successful birds in the arid regions of western North America. Its distribution is, however, sharply localized about water holes. Apparently this species is successful in deserts not because of any special physiological capacities, but because it can find locally favorable situations which allow it to survive and reproduce despite its extravagant needs for water.

A similar case is presented by the ploceid, *Passer domesticus*. The birds of this species in North America are derived from individuals introduced from the cool and moist British Isles and from Germany, but populations have been able to establish themselves in the severe deserts of southwestern North America wherever surface water is available. As Grinnell (1919) pointed out, this species has successfully invaded Death Valley, California, probably the most extreme desert area in North America. Many other species occupy deserts in a similar way, but there also appear to be varying degrees of independence from surface water among closely related species in arid environments (see Irwin, 1956), which suggests the existence of evolutionary trends among some groups of birds toward more specific adaptations for desert existence.

From the geological point of view, the widespread desert regions of western United States are relatively recent (Pliocene and Pleistocene) environments (Axelrod, 1950; Schwarzbach, 1961). Thus it is not unexpected that some species, such as the House Finch, which can live in these deserts show no special adaptations in water economy when compared with birds of more mesic environments. Indeed, Miller (1951) indicates that of the 274 species of birds which breed in California, only 17 show a primary affinity for the desert scrub habitat and 23 additional species occupy desert scrub only as a part of their distribution. Thus about 60 per cent of the desert scrub avifauna of California consists of species which cannot be characterized as primarily desert birds (Bartholomew and Cade, 1956).

The difficulty of showing a close correlation between arid environments in western North America and the water economy of the birds living there

is further illustrated by comparison of the Mourning Dove with the California Quail. As shown in Table 4, the California Quail is conspicuously better adjusted physiologically both to limited intake of water and to drinking salt water than is the Mourning Dove. Nevertheless, the quail is confined to brushlands and grasslands on the margins of deserts, while the dove ranges widely throughout the desert itself. As pointed out by Bartholomew and MacMillen (1961: 512-513): "This physiological paradox is at least partially explicable in behavioral terms. The doves are powerful fliers that can readily travel many miles to water while quail are weak

TABLE 4
COMPARISON OF WATER ECONOMIES OF THE MOURNING DOVE AND THE CALIFORNIA QUAIL (FROM BARTHOLOMEW AND MACMILLEN, 1961)

	<i>Zenaidura</i>	<i>Lophortyx</i>
Water deprivation		
Mean daily loss expressed as per cent initial body weight per day	4.8	1.6
Mean per cent initial body weight at death	63.3	50.4
Mean days of survival	7.3	33.3
Water consumption		
Highest concentration of sea water on which body weight can usually be maintained (given as percentage)	25	50
Mean daily <i>ad libitum</i> consumption of distilled water expressed as per cent body weight per day	9.9	5.2

fliers that are hardly more mobile than a medium-sized mammal. Hence, if this quail is to occupy even semidesert regions, it needs to be physiologically better adapted to aridity than the dove, despite the fact that the dove successfully occupies the desert while the quail cannot." Other species of quail, *Lophortyx gambelii* in particular, appear to have extended this physiological adjustment to aridity even further—to the point of becoming virtually independent of surface water and of living in desert valleys far from water. The presence of populations of these better-adapted quail may be another reason why the California Quail is restricted to the periphery of the desert.

Unfortunately, the maximum departure from the general avian pattern of water economy shown by North American desert birds has yet to be ascertained, because the most critical species have not been studied. For example, nothing is known about the water economy of such forms as the Black-throated Sparrow (*Amphispiza bilineata*) or the Rock Wren (*Salpinctes obsoletus*), neither of which appears to be dependent upon surface water.

Udvardy (1958) has pointed out that the North American scrub avifauna shows no close phylogenetic relationship with the xerophilic avifaunas of the great Palaearctic deserts. The same conclusion also applies obviously to Australia and Africa. He suggests that since the desert avifaunas of the Old World are much better developed than in the New World, the former are probably of greater antiquity and have had a longer period of time to become adaptively specialized for desert conditions. In this regard it is interesting to note that recent paleoclimatological studies suggest that desert conditions were present in parts of the Palaearctic by late Miocene time (Schwarzbach, 1961). The desert birds of the Old World could, therefore, reasonably be expected to show more conspicuous physiological adaptations to arid conditions than their ecological counterparts in the New World. Data on the Budgerygah (Cade and Dybas, 1962) and the unpublished physiological data on estrildine finches previously referred to in this review are consistent with this idea, and it is highly desirable that studies on the water economy of other Old World xerophilous psittacines, and granivorous estrildine and ploceine finches be carried out.

Because of the unusual composition of the terrestrial vertebrate fauna of Australia, study of adaptations of the desert birds there should be particularly interesting. It is the experience of the senior author and of other biologists who have worked in the arid parts of Australia that small seed-eating birds are relatively abundant there, and that small mammals, both placental and marsupial, are exceedingly scarce. The intriguing possibility exists that in Australia the situation with regard to desert vertebrates is the opposite of that found in North America, with birds (in this case, finches and parrots) being the dominant forms and mammals the less successful forms. If true, this would be consistent with Australian zoogeographic history, for even though Australia has a well-developed endemic rodent fauna (Simpson, 1961), the rodents are relatively late arrivals on the Australian scene as compared with birds.

Ecological patterns of water economy in desert birds.—The least specialized and most restrictive pattern of water economy for desert occupancy is typified by the House Finch and the House Sparrow, which are closely dependent upon surface water at all times. Such species never venture far away from water and must return to it for repeated drinks throughout the day—especially during times when the air temperature is hot enough to require extensive evaporative cooling by a small bird. These water-dependent populations are also restricted in the area available to them for foraging, since they cannot feed in localities beyond the daily, or even hourly, cruising range away from water. According to Irwin's (1956) observations many small finches in the Kalahari are similarly restricted to the environs around water holes.

A second ecological pattern is that shown by the Mourning Dove. This bird is still dependent upon surface water for drinking, but because of its great mobility and its capacity to hold large quantities of water in the alimentary tract, it needs to drink only once or twice a day and can spend the rest of its time foraging in areas far removed from water. The dove is thus able to exploit more of the desert environment than is a bird like the House Finch. Many species of doves, sandgrouse, parrots, and some passerines apparently conform to this pattern; and the great flocks of these birds which have been observed at isolated water holes in various deserts of the world attest to the effectiveness of this way of life in the arid lands. Not all of these species have the same capacity as the Mourning Dove or sandgrouse to drink a large volume of water in a single draught or two, and such species, particularly small ones, have developed special abilities to prevent excessive loss of water (Cade and Dybas, 1962).

A third pattern is exemplified by the various carnivorous and insectivorous birds, which obtain all the water they need from their highly succulent foods. The occupation of desert areas by such species is not restricted by sources of potable water, and generally speaking it is these species which occur most commonly in waterless regions. In the case of birds which are primarily granivorous, independence of water is difficult to achieve because their food contains only about 10 per cent moisture or less. Even so, populations of some small, granivorous forms like the fringillid, *Amphispiza bilineata*, in the deserts of western North America and like the ploceids, *Sporpipes squamifrons* and *Anaplectes melanotis* (= *Malimbus rubriceps* of Peters' Check-List, vol. XV), in the Kalahari Desert (Irwin, 1956) appear seldom or never to visit surface water. Presumably such species augment their grain diet with enough succulent vegetable and animal foods to maintain water balance, but recent evidence (reviewed above) also indicates that some of these granivorous birds (*Passerculus sandwichensis*, *Melospittacus undulatus*, *Taeniopygia castanotis*) have become adaptively modified to reduce water losses sufficiently to survive for many days, at least at moderate temperatures and humidities, on a diet of dry seeds without drinking. Although none of these species appears to be physiologically as well adapted to live without water as some of the desert rodents, their performances are nonetheless remarkable in view of the fact that they do not escape from the daytime conditions of the desert, as the rodents do.

The utilization of saline water.—Most land birds probably are unable to maintain water balance on aqueous solutions much more concentrated than their own body fluids, and consequently the sea and highly saline inland waters are of no use to these birds. Among North American species, however, it is interesting that the most conspicuous departure from

the general avian pattern of water economy so far found is shown by the salt marsh-inhabiting races of the Savannah Sparrow, which can drink sea water successfully. Although these birds range into desert regions, they are primarily associated with coastal areas. Coastal salt marshes, in contrast with the New World deserts, are habitats of great antiquity. The salt marshes of Baja California and Sonora, Mexico, are often bounded by severe deserts, and Cade and Bartholomew (1959) have suggested that the long occupancy of salt marshes, in which fresh water is scarce, has favored the evolution of physiological capacities preadaptive for living under desert conditions.

Since the desert-adapted renal functions of a kangaroo rat permit it to drink sea water (B. and K. Schmidt-Nielsen, 1950b), it seems likely that the reciprocal is true for Savannah Sparrows: a kidney originally adapted to process a high intake of salt is also adaptive for a minimal intake of water. In this connection, it is worth noting that *P. s. rostratus* is better able to withstand deprivation of water after a period of drinking sea water than it is after a period of drinking distilled water (Cade and Bartholomew, 1959). On the other hand, the ability of a xerophile like the Zebra Finch to maintain water balance while drinking aqueous solutions of NaCl as concentrated as 0.6 M (Oksche, Farner, Serventy, Wolff, and Nicholls, 1963) probably is, like the case of the kangaroo rat, a secondary characteristic of renal functions which evolved in response to low water intake. Be that as it may, among the species listed in Table 2 there is a close correspondence between ability to maintain weight when drinking hyperosmotic aqueous solutions and ability to maintain weight when deprived of water. The mechanism underlying these abilities needs study.

From an ecological point of view, it is interesting that various populations of Savannah Sparrows breeding in Baja California and Sonora, Mexico, have successfully established themselves on waterless desert islands: *P. s. beldingi* breeds on Islas Todos Santos and *P. s. sanctorum* breeds on the San Benitos (van Rossem, 1947). On the mainland of Mexico in the salt marshes of Sonora, *P. s. rostratus* breeds under some of the most extreme conditions of heat, aridity, and lack of fresh water to be found in North America.

RESEARCH PROBLEMS

The clearest message we hope to impart by this review is that not much is known about the water economy of land birds. This gap in ornithological knowledge should not be difficult to fill, and many attractive problems suggest themselves. The simple determinations of rates of dehydration, *ad libitum* water consumption, or minimum daily water ration required for maintenance of body weight for any bird held on a dry diet

under known conditions of temperature and humidity would represent useful contributions to the subject. Such measurements are easily within the technical ability of an interested undergraduate zoology student, and none requires much more than patience and careful bookkeeping. As indicated above, small parrots and Old World, African, or Australian finches offer great potentialities for new insights into the problem of reconciling the extravagant evaporative water loss of small birds to existence on a minimum intake of water. The smaller doves and the bustard-quails (*Turnicidae*) also present attractive possibilities. Many of these birds are available from avicultural sources, and even domesticated strains should amply repay investigation. Little is known about the role of taste in the biology of birds. Tests of a bird's ability to discriminate between various naturally occurring waters in its habitat or between experimentally varied drinking solutions could assist in understanding some aspects of avian water economy.

At a slightly more complex level, but with essentially the same methods, the effects of salinity, temperature, humidity, or other physical and chemical factors on the parameters mentioned above can be studied, and such research would contribute significantly to knowledge of comparative avian physiology. At a still more technical level, measurements of the osmotic pressures and electrolyte concentrations in birds from a variety of taxonomic groups and habitats are highly desirable; virtually no comparative data on these topics are now available. Likewise, there are few comparative data on the histology of the kidney of birds. Apparently no one has ever looked at the kidneys of a variety of birds from the standpoint of correlating microanatomy and function, as Sperber (1944) has done for rodents. There is a closely related anatomical topic which to our knowledge has not been investigated at all—the possible existence of microanatomical specializations in the cloaca or lower gut which might be associated with a capacity for fluid resorption or salt excretion.

Other more complex investigations suggest themselves also. It would be interesting to apply the method of ethanol dilution employed by Budtz-Olsen, Cleeve, and Oelrichs (1961) to the determination of the total body water of birds under different conditions of hydration. It would be instructive to use tritiated water to determine the rate of water turnover of captive birds and of wild birds which are released and recaptured. This method has been applied to captive kangaroo rats by Richmond, Trujillo, and Martin (1960). More studies need to be carried out on the interrelations between metabolic rate, ambient temperature, and respiratory water loss; simultaneous measurements of metabolic rate and respiratory water loss over a range of ambient conditions are available for only three or four species.

The most important contributions of all from an ecological point of view can be made by careful and detailed field studies of birds in arid or desert areas. Which species known to exist in a given area do not visit water? How often does a given individual visit water? Does the frequency vary with weather, season, and breeding activities? Irwin's (1956) meaty little article on the drinking habits of birds in Bechuanaland gives an indication of the fruitfulness of this approach. Prolonged observations at isolated water holes, of the sort attempted by Bartholomew and Dawson (1954), should be repeated and extended. Careful appraisals of the birds in a desert region like that reported by Johnson, Bryant, and Miller (1948) for the Providence Mountains in the Mohave Desert of California, or that by Hensley (1954) for southern Arizona, should be carried out in other areas.

Physical measurements of the environment can usefully be applied to behavioral and ecological studies. For example, measurements of the temperature, humidity, and air movements adjacent to and within nest chambers or holes of species such as Verdins, Ladder-backed Woodpeckers (*Dendrocopos scalaris*), and Elf Owls (*Micrathene whitneyi*) should be undertaken in relation to time of day and season. Some of the methods of Kendeigh (1961) should be applicable and would assist greatly in understanding the ways in which birds can ameliorate the effects of the desert environment by their activities and habits.

Observational studies are needed on desert birds to determine the ways in which they respond behaviorally to high temperatures and to scarcity of water. Do thrashers or towhees resort to rodent burrows during the heat of the day? What use of the shelter afforded by rock crevices do Rock Wrens make? Are there seasonal shifts to more succulent foods during the dry season as compared with the wet season? These and many other intriguing questions are waiting to be answered.

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