WATER ECONOMY OF GRANIVOROUS BIRDS:
A PREDICTIVE MODEL[1]

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Abstract. A model has been devised by which to explore the efficiency of metabolic usage of seeds by granivorous birds in meeting simultaneously their water and energy needs. It is based on the premise that physiological specializations have occurred that enhance granivory, and that these, in turn, promote ecological freedom in foraging for a single resource (seeds) to meet water and energy needs rather than reliance upon two spatially and temporally separate resources. The model predicts that, if sufficient seeds are available, energy needs will be met, but that water needs may be met concomitantly through metabolic water production only by the existence of appropriate combinations of body mass, ambient temperature, and watering histories of the birds. According to the model positive water balance is achieved when these combinations result in rates of metabolic water production ≥ evaporative water loss. The model predicts further that smaller (in mass) birds will more readily attain favorable states of water balance on a seed diet and under arid conditions than will larger birds, and that this phenomenon will apply independently of taxonomic affinity.

Key words: Granivorous birds; water economy; metabolic water production; evaporative water loss.

INTRODUCTION

Granivory is trophically an important way of life for primary consumers in arid ecosystems around the world, and diverse communities of granivores have emerged made up principally of ants, rodents, and birds (Brown et al. 1979). While the precise trophic role of granivorous birds has proven elusive to assess directly (Brown et al. 1975, Morton 1985), indirect assessments based upon population densities, dietary habits, and energetic requirements indicate that birds are at least equal in importance to ants and rodents as consumers of seeds in North American and Australian arid zones (Pulliam and Brand 1975, Morton and Davies 1983, Parmenter et al. 1984).

It is reasonable to assume that specializations for granivory in birds have accompanied the development of their trophic importance, and that these include a suite of morphological, behavioral, and physiological attributes. The former two categories of specializations are readily observable and measurable, and are beyond the scope of this paper; it is the physiological specialization for granivory that interests me, particularly the interplay between water regulation

and energy regulation while subsisting on a diet of seeds. An examination of the role of this interplay in granivorous heteromyid rodents was prompted by an essay by Bartholomew (1972) on the water economy of granivorous birds that survive without drinking; we (MacMillen and Hinds 1983a) speculated that certain endothermic regulatory principles should apply equally to granivorous mammals and birds, and proceeded to model and document the water economies of heteromyid rodents based upon these principles. This mammalian model was proven to be very robust upon application (MacMillen and Hinds 1983a). It stands to reason that notions gleaned from an essay on granivorous birds (Bartholomew 1972) that have been used to clarify the water relations of granivorous mammals, might also be applied profitably to further the understanding of the water economies of the organisms on which they were originally based. Herein I apply these notions to granivorous birds by proposing a formal model to aid in the further investigation of their water economies.

DEVELOPMENT OF THE MODEL

Considerable attention has been paid to the topic of water regulation in birds during the past 18 years (Shoemaker 1972, Willoughby and Peaker 1979, Skadhauge 1981, Sturkie 1986), and the contributions by Willoughby and Peaker (1979)

TABLE 1.   Water budgets of certain seed-eating birds maintaining positive water balance while water-deprived or drinking their minimal water requirement, and subsisting on seeds (after Willoughby and Peaker 1979).

Species	Mass, g	Watering regime	Water input, % of total		Water output, % of total	
			Meta-bolic	Pre-formed	Evapo-rative	Cloacal
Zebra Finch (*Poephila guttata*)	12.7	deprived	78	22	64	36
Grey-backed Finch-Lark (*Eremopteryx verticalis*)	17.0	minimal	59	43	84	16
Budgerygah (*Melopsitticus undulatus*)	30.0	deprived	80	20	65	35
Mean	19.9		72	28	71	29

and Skadhauge (1981), in particular, have addressed the issue of water economy in granivorous birds. However, each of these works stressed the avian renal-cloacal complex as the most important regulatory system contributing to the achievement of water balance. I agree that this complex is extremely important in modulating water loss through excretion and defecation and that its intensive study has been justified. However, when granivorous birds are water-stressed but still in positive water balance, and with the renal-cloacal complex operating at maximal efficiency in water conservation, the combined loss of water in the urine and feces accounts only for about 30% of the total that is lost (Table 1). The major avenue of water loss under these conditions is that of evaporation (termed evaporative water loss, EWL), accounting for about 70% of the total (Table 1). On the input side of a water balance scheme in such birds is a small proportion (ca. 30%) representing preformed water (absorbed in the seeds, drunk) and a much larger proportion (ca. 70%) constituting metabolic water production (MWP; Table 1). Clearly, if the renal-cloacal complex serves as an osmoregulatory modulator in birds in general, and in granivorous birds in particular, its success is highly dependent upon the two major variables in the water budget scheme: EWL and MWP (Table 1). It is also important to emphasize that under laboratory conditions of water stress but with simultaneous achievement of water balance, the two major variables of water input and output are equal (MWP = EWL), and therefore their measure should represent a valid assay of the state of water balance. Since metabolic water production is a direct product of energy metabolism, and evaporative water loss figures prominently in the heat and energy budgets of birds (Weathers 1981), there must be continuous interplay between water

regulation and energy regulation with the two regulatory systems operating in concert.

Our work with heteromyid rodents (Morton et al. 1980; Thompson et al. 1980; Morton and MacMillen 1982; MacMillen 1983a; MacMillen and Hinds 1983a, 1983b; Hinds and MacMillen 1985) has demonstrated that highly integrated interrelationships between water and energy regulation, coupled with nocturnality (a behavioral component), and locomoter mode (bipedality vs. quadrupedality) and body size (both morphological components), provide the unique suite of adaptive characters that have promoted the specialization of granivory in this taxon of rodents. I have no doubt that parallel adaptive suites of characters have evolved that similarly promote granivory in several bird taxa, but synthetic studies are required to elucidate the efficiencies by which seeds may be used as a nutritional resource; particularly important to such studies would be attention paid to physiological performance at a taxonomic level above the species, and concomitant assessments of the role (or consequences) of body mass differences. Understandably, environmental physiology had its roots in species-specific studies that aimed at elucidating unique attributes of individual species populations. For birds, earlier syntheses were undertaken by relatively few, imaginative workers who gleaned general patterns and principles from a myriad of independent studies. Examples of such important synthetic reviews that apply to granivorous birds include that on the water economy of land birds by Bartholomew and Cade (1963), that on water independence in granivorous birds by Bartholomew (1972), and that on the physiological ecology of desert birds by Dawson (1974). The former review (Bartholomew and Cade 1963) describes the physical and physiological problems faced by granivorous birds, but

provides only the incomplete answers that were available at the time. A much more provocative paper is Bartholomew's (1972) synthesis of 15 separate papers (only two of which were available for the earlier review), describing the ability of certain small, granivorous birds to survive in the laboratory on a diet of air-dried seeds and without drinking water, a feat previously known among endotherms only for certain granivorous rodents; the synthetic importance of this paper is that it provides the framework of a still-to-be formulated predictive model to explain the occurrence and probability of such water independence in granivorous birds. Dawson's (1974) review updates the published information on granivorous birds, reiterates the elements of Bartholomew's (1972) model of water independence, and adds three Australian parrot species to the list of water-independent granivorous birds. These synthesizers provide the framework for testable models to elucidate the extent to which physiological performance has been molded, relative to body mass, to promote efficiency in the utilization of seeds as a nutritional resource.

The lives of organisms can be appreciably simplified if, in the process of foraging, all or most of the nutritional needs can be met by a single resource packet, such that separate foraging ventures for energy and water (and likely also minerals and vitamins) are minimized. We (MacMillen and Christopher 1975) concluded that such is the case for desert rodents, regardless of diet, and demonstrated how this can be accomplished both by omnivorous (MacMillen 1983b, MacMillen and Garland 1989) and granivorous rodents (MacMillen and Hinds 1983a). The possibility of meeting both energy and water requirements by election of an appropriate food item is enhanced for rodents by their habits of fossoriality during the day and nocturnal activity. These habits minimize water expenditures to the extent that in granivorous heteromyids MWP from the oxidation of seeds is sufficient under most microenvironmental conditions to offset most if not all water expenditures (MacMillen and Hinds 1983a). Granivorous birds on the other hand are diurnally active, and roost at night aboveground and thereby are exposed much more directly to ambient surface or above-surface conditions around the clock; thus their habits expose them to physical conditions that could result in potentially greater water expenditures.

To what extent can granivorous birds utilize a single food packet, seeds, to meet both their energy and water needs (or, do granivorous birds possess unusual metabolic processes that promote specializations for granivory)? An early negative answer to this question was seemingly provided by Bartholomew and Dawson (1953), and again by Bartholomew and Cade (1963); they demonstrated with the information available at the time that, even in the absence of heat stress, the rate of EWL in birds of up to 150 g in body mass (and regardless of diet) exceeds the rate of metabolic water production; birds between 40 and 150 g had the least excess, and birds between 10 and 30 g had substantial to enormous excesses. Implied in these studies is the expectation that if water-independent granivorous birds (in which MWP > EWL) exist, they should exceed 40 g in body mass. The granivorous Mourning Dove (*Zenaida macroura,* ca. 120 g) appeared nearly able to offset EWL with MWP (Bartholomew and Dawson 1953), yet Bartholomew and MacMillen (1960) showed that it lost weight very rapidly (and fatally if prolonged) when held under laboratory conditions on a diet of air-dried seeds without drinking water. Since about 1960, however, an increasing number of granivorous birds has been demonstrated to be able to survive under laboratory conditions on a seed diet without drinking water; paradoxically, all of these are small, with a body mass of 30 g or smaller (Bartholomew 1972, Dawson 1974), and most less than 20 g.

Representative of these granivores that can survive on seeds without drinking water (and some that cannot) are members of the passerine family Fringillidae (conservative classification; see Sibley et al. 1988, and others for more liberal yet still controversial schemes) as illustrated in Figure 1. That the response of body mass to water deprivation may also be influenced by temperature (T_a) is illustrated by the Brewer's Sparrow, *Spizella breweri,* one of these water-independent fringillids (Fig. 2, data from Ohmart and Smith 1970). In addition, other such water-independent, small granivorous birds are members of the passerine families Estrildidae, Ploceidae, and Alaudidae, and Australian parrots of the family Platycercidae (Bartholomew 1972, Dawson 1974). This paradox that birds weighing less than 40 g should have rates of EWL considerably in excess of MWP (Bartholomew and Dawson 1953, Bartholomew and Cade 1963), yet it is only small,

TABLE 2. Lower critical temperatures (T_{LC}) and body masses of a variety of granivorous birds for which such data are available.

Family and species	Body mass, g	T_{LC}, °C	Source
Water independent			
Fringillidae			
Black-throated Sparrow (*Amphispiza bilineata*)	13.4	ca. 35	Bartholomew, pers. comm.
Estrildidae			
Silverbill Finch (*Lonchura malabarica*)	10.9	ca. 33	Willoughby 1969
Zebra Finch (*Poephila guttata*)	12	ca. 36	Cade et al. 1965
Platycercidae			
Budgerygah (*Melopsitticus undulatus*)	30	34	Greenwald et al. 1967
Water dependent			
Fringillidae			
White-crowned Sparrow (*Zonotrichia leucophrys*)	28.6	23	King 1964
Pyrrhuloxia (*Cardinalis sinuata*)	32.0	30	Hinds and Calder 1973
Cardinal (*Cardinalis cardinalis*)	41.3	29	Hinds and Calder 1973
Brown Towhee (*Pipilo fuscus*)	43.7	23	Dawson 1954
Abert Towhee (*Pipilo aberti*)	46.8	25	Dawson 1954
Estrildidae			
Black-rumped Waxbill (*Estrilda troglodytes*)	6.1	28	Lasiewski et al. 1964
Columbidae			
Inca Dove (*Columbina inca*)	41.5	33	MacMillen and Trost 1967

granivorous birds (<30 g) that can survive on dry seeds without drinking water, can apparently be explained by an erroneous (but understandable) assumption on which Bartholomew and Dawson's (1953) interpretations were based. They (Bartholomew and Dawson 1953) assumed that, regardless of size, the experimental temperature of 25°C was within the zone of thermal neutrality, and therefore estimates of MWP based upon predicted basal metabolic rates were appropriate for comparisons with measured levels of EWL at that T_a. It has since become apparent that lower critical temperatures (T_{LC}, the lower limits of thermal neutrality) of these small granivorous birds that survive without drinking water are well above 25°C (Table 2), and therefore the estimates of MWP were far too low. Such high lower critical temperatures imply correspondingly high levels of heat exchange with the environment (high rate of thermal conductance or heat transfer coefficient = less effective insulation), translating into increased slopes of energy metabolism as a function of ambient temperature below thermal neutrality. These increased levels of heat exchange (usually measurable as rates of oxygen consumption) represent increased energetic cost (usually viewed as a disadvantage) and increased

MWP (herein viewed as an advantage), suggesting the possibility of trade-offs between energetic expenditure and metabolic water production. The models and allometric analyses of endothermic thermoregulation all reveal the expectation that small birds have high mass-relative standard metabolic rates, high lower critical temperatures (and short thermal neutral zones), and steep slopes of energy metabolism below thermal neutrality, while large birds show the converse relationships (see Calder and King 1974, for recent discussion). The empirical data on which the allometric analyses are based confirm these models, but reveal considerable individual species variability. With regard to the relationship between body mass and position of the lower critical temperature this variability is particularly apparent, leading Calder and King (1974) to comment: "Thus, although common sense tells us that the smaller the bird, the smaller its thermal inertia, and hence the smaller its zone of thermoneutrality, the determination of T_{LC} incorporates variabilities in basal metabolism, the cold-stress regression line, and any possible adaptation to the environment, so that it is difficult to show the expected correlation between bird size and T_{LC}." It is apparent from Figure 1 and Table 2
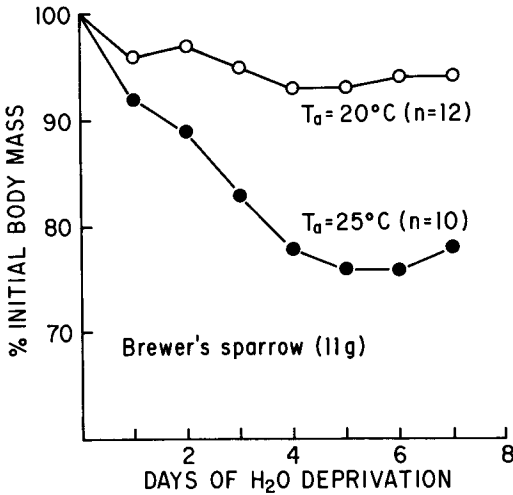
FIGURE 1.   The response of body mass to water deprivation in seven species of granivorous, fringillid birds. All birds were maintained under comparable conditions of moderate humidity (40–70%) and temperature (ca. 25°C). With the exception of Sage Sparrows and White-crowned Sparrows, the birds were maintained on mixed birdseed (largely millet) for food; the former two species were maintained on chick starter mash. Data from Bartholomew and Cade (1956), MacMillen and Snelling (1966), Smyth and Bartholomew (1966), Moldenhauer and Wiens (1970), Ohmart and Smith (1970, 1971), and Dawson et al. (1979).
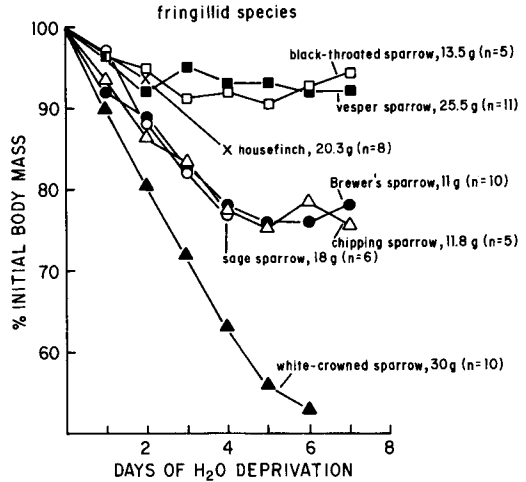

FIGURE 2.   The response of body mass to water deprivation in Brewer's Sparrows held at 20°C and 25°C; otherwise conditions as in Figure 1. Data from Ohmart and Smith (1970).

that all water-independent granivorous birds are small, but that not all small granivorous birds are water-independent; correspondingly all water-independent granivorous birds have $T_{LC} > 30°C$, but the smallest granivore in this table (Black-rumped Waxbill, *Estrilda troglodytes*, 6.1 g) is not water-independent and has a $T_{LC} = 28°C$. Thus, I view the precise position of T_{LC} among small birds to be variable and subject to adaptation, and that a high T_{LC} in granivorous birds represents an adaptation that enhances water regulatory efficiency through increased MWP at the expense of increased energetic cost.

Intuitively, since a major component of evaporative water loss is respiratory, and respiratory rate is linked directly to energy metabolism, one would assume that curves of energy metabolism and EWL in endotherms would be parallel. However, unlike energy metabolism and MWP, EWL tends to decline with decreasing T_a within and below thermal neutrality. This is presumably because of a nasal heat-exchange system in both birds and mammals that results in progressive cooling and saturation of expired air (Schmidt-

Nielsen et al. 1970). Thus, as Bartholomew (1972) remarks, EWL and MWP become uncoupled below T_{LC}. This uncoupling is demonstrated in Figure 3 for two species of xerophilous granivorous birds, the Australian estrildid Zebra Finch (*Poephila guttata,* 12 g; Cade et al. 1965) and the North American Inca Dove (*Columbina inca,* 41.5 g; MacMillen and Trost 1967). Thus, below thermal neutrality, with MWP having a negative slope and EWL having a positive to neutral slope, some thermal point below thermal neutrality must exist for each species at which the two curves intersect and MWP = EWL; below this point is the approximate thermal region of positive water balance even without drinking, and above this point negative water balance is incurred unless drinking occurs. The position of this thermal point of intersection and the thermal environment in which the bird exists determine the extent to which these relationships are ecologically relevant. It should be obvious that a high thermal point of intersection confers maximal water regulatory efficiency (i.e., greater degrees of water independence).

Similar to the relationship in heteromyid rodents (MacMillen and Hinds 1983a) the ratio MWP:EWL in birds, when expressed as a function of T_a on a semilogarithmic plot, assumes linearity lending itself to regression analysis (Fig. 4). By this analysis the thermal point at which MWP = EWL (as used by MacMillen and Hinds
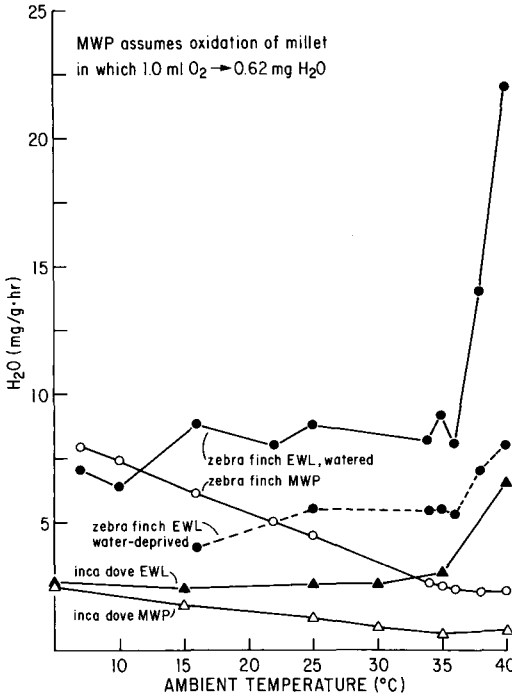
FIGURE 3. The relationships between evaporative water loss (EWL) and metabolic water production (MWP) in watered and water-deprived Zebra Finches and in watered Inca Doves. MWP was calculated from measurement of oxygen consumption assuming oxidation of millet. Data from Cade et al. (1965) and MacMillen and Trost (1967).
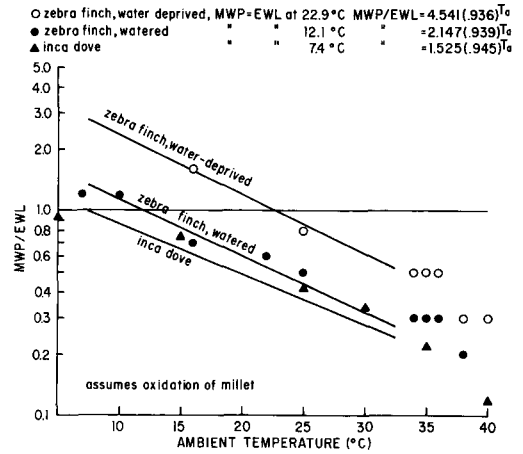

FIGURE 4. The semilogarithmic relationships between MWP/EWL and ambient temperature in watered and water-deprived Zebra Finches and in watered Inca Doves. Data from Figure 3. The horizontal line represents the condition of unity between MWP and EWL, and the thermal point of water regulatory efficiency (T_a at MWP = EWL) is defined as that point at which the diagonal regression line for each treatment intersects the horizontal line.

1983a, to represent an index of water regulatory efficiency) for each individual and population may be defined, allowing explicit statements concerning states of water balance as a function of thermal regimes. We assume, and with confidence, that if sufficient seed is available, a positive state of energy balance is maintained independent of T_a, and that it is the state of water balance that varies with T_a (as suggested for Brewer's Sparrows in Fig. 2). At all T_a's below this thermal index (T_a at MWP = EWL) positive states of both energy and water balance exist without the necessity of drinking water, augmented by any preformed water that may be in the food.

It is apparent in at least some granivorous birds, even with unchanging atmospheric humidity, that the rate of EWL is not constant at any one T_a, and varies with the accessibility of succulent foods and drinking water. This variability is demonstrated clearly with the Zebra Finch in Figure 3, in which the rate of EWL of water-deprived birds

averages across the T_a range of common measurement 54.4% that of the birds drinking water ad libitum. As can be seen in Figure 4 this reduction in EWL, without a concomitant alteration in MWP (none was apparent, Cade et al. 1965), results in a substantial upward shift of the thermal index from 12.1 to 22.9°C. Thus, it is easy to understand how Zebra Finches can be maintained under laboratory conditions of moderate temperatures and humidities on an air-dried seed diet (usually ca. 10% preformed water) without drinking water. Under these conditions, clearly, the Zebra Finch can meet both its water and energy needs with a single resource packet, seeds; this capacity is aided additionally by the avian uricotelic habit of excreting nitrogenous waste as a relatively dry precipitate, and by voiding feces with a very low water content (Lee and Schmidt-Nielsen 1971). Lee and Schmidt-Nielsen (1971) have also demonstrated that the reduction in EWL of water-deprived birds is not due primarily to a reduction in respiratory water loss, and therefore must be due to reductions in cutaneous water loss (Table 3). Not all granivorous birds capable of surviving without drinking water have significantly reduced EWL while water-deprived (Table 3), and so this capacity
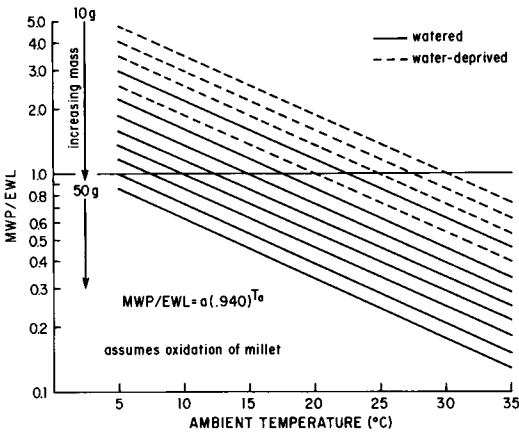
FIGURE 5. A model of the relationship between MWP/EWL and ambient temperature in granivorous birds. The horizontal line represents the condition of unity between MWP and EWL. The diagonal lines are the theoretical regression lines (slope of 0.940) for different-sized species, representing the semilogarithmic relationship between MWP/EWL and T_a. The solid diagonal lines represent the probable conditions for the larger species while watered; each dashed diagonal line represents a smaller, water-deprived species, or the next larger species in the watered state. The intercept of each diagonal line with the horizontal line represents the thermal index of water regulatory efficiency for each species as predicted by the equation MWP/EWL = $a(0.940)T_a$.

FIGURE 6. The theoretical relationships between the thermal index of water regulatory efficiency (T_a at MWP = EWL) and body mass in watered and water-deprived birds as predicted by the model depicted in Figure 7.

does not appear uniform even among the so-called water-independent species. Other than the suggestion that the reduction is in cutaneous EWL (Lee and Schmidt-Nielsen 1971), its mechanisms, extent, and frequencies of occurrence remain unknown. One might speculate that reductions in cutaneous EWL might result from changes in water permeability of avian skin that promote varying levels of water-vapor diffusion resistance, as has been noted in several species of columbiform birds when exposed to differing ambient temperatures (Webster and Bernstein 1987).

We are now in a position to formulate a testable model of water regulatory efficiency in granivorous birds, one that will reveal the extent to which seeds provide through oxidation the simultaneous energy and water needs of these consumers. The model, as hinted by Bartholomew (1972) and Dawson (1974) and modified from MacMillen and Hinds (1983a) for heteromyid rodents, is a mass-related one that accounts for states of water balance while oxidizing seeds in
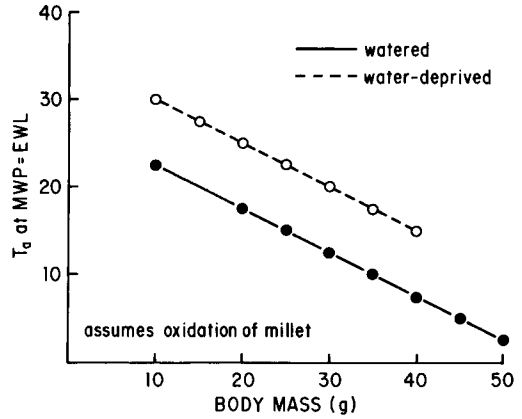
granivorous birds as functions of body mass, ambient temperature, and watering history (Figs. 5 and 6). In spite of Calder and King's (1974) precautions about the variability of the lower critical temperature in birds (and see Table 2), a mass-related model is the most conservative one and also the most sensible one from the perspective of energy exchange (Calder and King 1974, Calder 1984, Schmidt-Nielsen 1984). This model is patterned after the limited empirical data that are available (as in Fig. 4), and predicts that the extent to which a granivorous bird can meet its metabolic needs from seeds (such as millet) varies with T_a and watering history, and that the semilogarithmic relationships relating MWP/EWL to T_a possess negative parallel slopes (0.940 as approximated from the data in Fig. 4); the model predicts further that the thermal index of water regulatory efficiency (T_a at MWP = EWL) will scale arithmetically and negatively with body mass, and that at least some birds deprived of drinking water will yield a separate, even more favorable distribution with regard to indices of water regulatory efficiency by reducing EWL (Fig. 6). An additional assumption of the model is that it reflects conditions of very low atmospheric humidities (comparable to dry-desert conditions), and that tests of the model will employ similar conditions by using open-airflow respirometry systems and appropriate airflow rates as described by Lasiewski et al. (1966). Such conditions result in maximal rates of EWL, and often exceed in terms of water loss those actually en-

TABLE 3. Mean rates of evaporative water loss (EWL) of several species of birds capable of surviving on a dry-seed diet without drinking water and under laboratory conditons. The measurements were made on watered and water-deprived individuals at $T_a = 25°C$.

Species	Body mass, g	Watered EWL, mg/g·hr		Water-deprived EWL, mg/g·hr		Source
		Com-bined[a]	Respira-tory	Com-bined[a]	Respira-tory	
Zebra Finch	12.0	8.80		5.50[b]		Cade et al. 1965
Zebra Finch	11.5	6.85	3.57	4.13[b]	3.02	Lee and Schmidt-Nielsen 1971
Brewer's Sparrow	11.0	4.62		2.05[b]		Dawson et al. 1979
Chipping Sparrow	11.8	2.76		2.50		Dawson et al. 1979
Budgerygah	30.0	5.00		4.30		Greenwald et al. 1967

[a] Combined EWL = cutaneous and respiratory EWL.
[b] Combined EWL of water-deprived birds is significantly lower than that of watered birds.

countered in nature by the experimental subjects. Thus the model predicts performance under the most xeric conditions that might be encountered.

Although conservative, the model is also versatile in its potential applicability within and between avian granivorous taxa and across virtually any range in body mass. Although not addressed directly, it can also accommodate any circadian differences in MWP and EWL such as are known to exist for energy metabolism (and therefore MWP; Aschoff and Pohl 1970). It does assume that a constant relationship exists between MWP and EWL regardless of level of activity (as confirmed by data extracted from Paladino and King 1984, for hopping White-crowned Sparrows, *Zonotrichia leucophrys*; Table 4), and that MWP is a direct reflection of metabolic rate and the composition (carbohydrate:lipid:protein) of the seeds being oxidized. The model is based upon the oxidation of millet seed (81.4% carbohydrate:5.1% lipid:13.5% protein; 1 ml O_2 yields 0.62 mg MWP; MacMillen and Hinds 1983a), but can be adjusted to accommodate seeds of any known composition.

It is unfortunate that no appropriate direct measures of energy metabolism and EWL have been made in flying birds that would allow accurate extrapolations of MWP/EWL for activity beyond the values of Paladino and King (1984) for hopping birds. However, the few data that are available are suggestive and conform to my expectation. Energy metabolism in flight has been measured in the Budgerygah (*Melopsittacus undulatus*, 30–40 g) by Tucker (1968) and the Fish Crow (*Corvus ossifragus*, 280 g) by Bernstein (1976). While Tucker's (1968) measures of oxygen consumption were direct, his simultaneous measures of EWL were indirect, based upon changes in body mass during flight. Bernstein's (1976) measures of oxygen consumption during flight were also direct, as were his measures of respiratory water loss, however he did not measure cutaneous water loss and therefore the relationship between MWP and EWL during flight is unknown. These flight data are summarized in Table 5, and indicate that, as in rest, there is a negative relationship between MWP/EWL and T_a, but the data are too incomplete to consider flight speed as a variable. It is interesting however that in the Budgerygah the ratio of MWP:

TABLE 4. The relationships between metabolic water production/evaporative water loss (MWP/EWL), ambient temperature, and hopping speed in Gambel's White-crowned Sparrow (after Paladino and King 1984). MWP based on the oxidation of millet, and assumes 1 ml O_2 yields 0.62 mg H_2O.

T,°C	Hopping speed[a]				
	Resting MWP/EWL	0.30 km/hr MWP/EWL	0.35 km/hr MWP/EWL	0.41 km/hr MWP/EWL	0.46 km/hr MWP/EWL
25	0.43	0.46	0.40	0.42	0.47
12	0.58	0.64	0.62	0.67	0.61
0	1.00	1.23	1.02	0.87	1.04
−10	2.37	2.56	2.50	2.52	2.46

[a] Mimics slower speeds of movement in nature.

EWL at about 20°C at rest and while flying at 35 km/hr is the same (0.67, Table 5); this is similar to the constancy of that ratio for resting and hopping White-crowned Sparrows (Table 4), again suggesting that these resting values may also reflect activity states.

Although devised for granivorous birds, this model applies with equal accuracy to any bird as long as the dietary composition (carbohydrate : lipid : protein) is known, and adjustments are made for preformed water intake. Thus it can accommodate insectivorous, nectarivorous, and frugivorous birds, too; these, though, typically subsist on foods whose preformed water contents are sufficiently high that the oxidative water yield is likely to be of lesser importance. What I am designating as granivorous birds often consume large quantities of insects, fruits, and green vegetation during particular seasons and periods, but it is the periods in which these are relatively unavailable (late summer, fall, winter, and particularly in arid settings) that the model is most applicable, and it is these same periods that likely have shaped these regulatory processes over evolutionary time. The model predicts that for each species, some temperature exists below which positive water balance can be maintained exclusively through metabolic water production, even while breathing exceedingly dry air. It predicts further that a given species of granivorous bird should be in a more favorable state of water balance at a lower T_a than at a higher T_a. These predictions appear to be confirmed by the performance of Brewer's Sparrows when kept on a dry-seed diet at $T_a = 25°C$ and $20°C$ (Fig. 2, data from Ohmart and Smith 1970); weight maintenance is much more readily attained at the lower T_a than at the higher T_a, although adjustments (reductions in EWL, Dawson et al. 1979) occur that eventually result in weight maintenance without drinking water at both T_a's.

ECOLOGICAL RELEVANCE OF THE RELATIONSHIPS BETWEEN MWP AND EWL

I do not contend that those birds capable of surviving in the laboratory on a seed diet without drinking water are completely or necessarily even largely independent of dietary preformed water in nature. I do contend that these birds represent one end of a spectrum of largely granivorous birds whose foraging capabilities and efficiencies are enhanced by reliance upon a specialized food

TABLE 5. The relationships between metabolic water production/evaporative water loss (MWP/EWL), ambient temperature, and flight speed in the Budgerygah and the Fish Crow. MWP based on the oxidation of millet, and assumes 1 ml O_2 yields 0.62 mg H_2O.

Flight speed, km/hr	T_a°C	MWP/EWL
Budgerygah (Tucker 1968)		
0	18–20	0.67
35	18–20	0.67
35	29–31	0.55
35	36–37	0.21
Fish Crow (Bernstein 1976)		
27	23	0.61*
27	28	0.37*
40	23	0.65*
40	28	0.40*

* EWL for Fish Crow based on measurement of respiratory evaporation alone; cutaneous evaporation not measured, and unknown.

resource—seeds—that is rich in energy and, under appropriate conditions of seed composition, atmospheric temperature and humidity, may concomitantly provide through metabolic water production assurance of positive water balance. Thus the relative luxury of specialization (granivory) results in focusing activity related to procurement of nourishment (food and water) on finding a single resource, rather than dividing time that may be costly in terms of both energy and water expenditures, and increased predation risk, into the two separate acts of finding energy and water. The economical state of water regulation of these granivorous birds means that even though negative states of water balance may accrue, they do so only slowly, with a return to positive water balance accomplished rapidly, and with relatively modest and infrequent intakes of preformed water in liquid form or in succulent foods required to reestablish a state of positive water balance.

My model of water regulatory efficiency of granivorous birds (Figs. 5 and 6) predicts that the smallest (by mass) members of a taxonomic group or feeding guild should be the best equipped to inhabit permanently xeric situations, particularly if they have the capacity of reducing EWL during periods of relative water stress. The model suggests further that progressively larger species of such groups are physiologically better suited for milder settings where higher humidity and precipitation result in reduced EWL, and readier access to food with higher preformed water con-

TABLE 6. The occurrences and body masses of representative North American fringillid and Australian psittaciform birds that are considered granivorous herein.

| | | Occurrence | | |
| | | California | | |
Family (order) and species	Body mass, g[a]	Joshua Tree (Desert)	Starr Ranch (Coastal)	Australian arid zone
Fringillidae (Passeriformes)				
Brewer's Sparrow (*Spizella breweri*)	11	X[b]		
Black-throated Sparrow (*Amphispiza bilineata*)	13	X		
Sage Sparrow (*Amphispiza belli*)	15	X[b]		
House Finch (*Carpodacus mexicanus*)	20	X	X	
White-crowned Sparrow (*Zonotrichia leucophrys*)	29	X[b]	X[b]	
Golden-crowned Sparrow (*Zonotrichia atricapilla*)	35	X[b]	X[b]	
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	38		X	
Brown Towhee (*Pipilo fuscus*)	44		X	
Platycercidae (Psittaciformes)				
Budgerygah (*Melopsitticus undulatus*)	30			X
Bourke's Parrot (*Neophema bourkii*)	39			X
Polytelitidae (Psittaciformes)				
Cockatiel (*Nymphicus hollandicus*)	81			X
Cacatuidae (Psittaciformes)				
Galah (*Cacatua roseicapilla*)	267			X

[a] Body masses of birds from Weathers (1983), Cade and Dybas (1962), Dawson (1965), Skadhauge (1974).
[b] Winter–spring residents only.

tents (as well as the greater availability of drinking water). Further, since the model is a temperature-dependent one, it predicts that at least intermediate-sized granivorous birds might successfully occupy the most xeric habitats during the winter periods of colder temperatures, during which more favorable relationships between MWP/EWL might permit positive water balance. These predictions are rather nicely confirmed by the distribution of species of the largely granivorous passerine family Fringillidae in southern California as suggested in Table 6. One of the smaller fringillids, the Black-throated Sparrow (*Amphispiza bilineata*; ca. 13 g) is a year-round resident of the hottest, driest desert habitats; intermediate-sized White-crowned Sparrows and Golden-crowned Sparrows (*Z. atricapilla*; 29 and 35 g, respectively) occur in harsh desert settings only during the cooler winter and spring; and still larger fringillids such as towhees (38–44 g) and grosbeaks (>40 g) occur only peripheral to the deserts and in more mesic montane and coastal situations (Weathers 1983, Miller and Stebbins 1964, pers. observ.). More enigmatic in distribution is the smallish (20 g) House Finch (*Carpodacus mexicanus*) that is a year-round resident of harsh desert settings, but apparently compensates for rather modest powers of metabolic water regulation with increased mobility and more frequent use of drinking water (Bartholomew and Cade 1963, Miller and Stebbins 1964).

While my model of water regulatory efficiency of granivorous birds is based largely upon a rather sparse body of data from passerine granivores, it does incorporate information from a small (ca. 42 g) desert granivorous dove (Columbiformes), the Inca Dove (Fig. 4), which appears to be in conformity with passerines. The extent to which this model applies specifically to granivorous passerines, and generally to granivorous birds independent of taxonomic affinity, is unknown, and therefore invites testing. For these reasons it is my intention to test the model with two major taxonomically and geographically distinct groups of granivorous birds that appear to share metabolic patterns in common: xerophilous fringillid passerines in North America and xerophilous parrots in Australia (Table 6). Of these parrots, the two smaller (by mass) species (the Budgerygah—30 g, and Bourke Parrot, *Neophema bourkii*—39 g) can both subsist in the laboratory without drinking water (Greenwald et al. 1967, Lindgren in Dawson 1974), and therefore suggest conformity to the model.

In all likelihood the low body mass of the most

successful desert granivorous birds imparts efficiencies both in water and energy regulation. At first sight this seems paradoxical because those small birds that have achieved the greatest degrees of preformed water independence have unusually high upper critical temperatures (Table 2), and therefore elevated mass-relative energetic costs even at moderate and certainly at low ambient temperatures; in a sense they have traded off efficiency in energy regulation for achieving greater efficiency in water regulation (increased MWP). The paradox is likely resolved by their small size which carries with it a reduction in absolute energy costs to levels more consistent with seed resource availability, even given the reduced rates of primary (and seed) production characteristic of arid regions. Thus efficiency in energy regulation is achieved by small size and correspondingly reduced absolute food requirements in spite of increased mass-relative rates of energy expenditure. It is altogether likely that constraints related to maintenance of water balance, energy balance, and seed size and dispersion, tempered by flight capabilities, act to set an upper limit on the body mass of granivorous birds that a given arid habitat may support at a particular time.

The model suggests moreover that this upper limit in body mass may change seasonally at a given locality with changes in thermal regimes, particularly in lower-latitude, low-elevation deserts. The merits of this suggestion are supported by Figure 7 which shows the isotherms of the index of water regulatory efficiency (that T_a at MWP = EWL) predicted by the model (Fig. 6) for a water-deprived 10-g granivorous bird, and a 30-g bird both in watered and water-deprived states, as compared to typical 24-hr air-temperature profiles for a midsummer (July) and a midwinter (January) day at a low-latitude desert site near Joshua Tree, San Bernardino County, California. If these predictions are accurate, and as long as suitable (by composition and abundance) seeds are accessible, overwintering granivorous birds up to and including 30 g in body mass should readily be able to maintain positive water balance without preformed water, so long as they are able to reduce EWL in the absence of drinking water. Even without such reductions in EWL the 30-g overwintering bird should face no more than 5 hr (hatched area A, Fig. 7) at midday during which MWP < EWL, requiring only modest amounts of preformed water to make up the def-
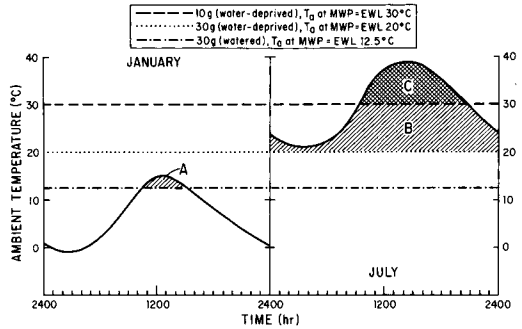

FIGURE 7. Stylistic but realistic 24-hr temperature profiles from Joshua Tree, California for a typical midwinter (January) and midsummer (July) day as measured in 1972 at a desert field site and in the habitat of those desert fringillid species identified in Table 6. The horizontal lines represent the thermal indices of water regulatory efficiency (T_a at MWP = EWL) for hypothetical 10- and 30-g birds (from Figs. 5 and 6), with separate lines for watered and water-deprived 30-g birds. That portion of the daily thermal profiles bearing hatched areas (A and B, diagonal lines) represents the time period for a 30-g bird in which MWP < EWL (negative water balance); that portion bearing cross-hatching (C) represents the time period for a 10-g bird in which MWP < EWL (negative water balance). See text for details.

icit. However, during midsummer (July) the 30-g bird should be in a continuous state of preformed water need (hatched area B, Fig. 7), and even the hypothetical 10-g bird with reduced EWL should experience a period of about 11 hr during midday (cross-hatched area C, Fig. 7) in which MWP < EWL, requiring some kind of compensation to achieve positive water balance over the 24-hr period. It is probably not fortuitous then that among the desert fringillids identified in Table 6, only the Black-throated Sparrow (ca. 13 g; rather sedentary) and the House Finch (ca. 20 g, probably highly mobile) are year-round residents of the site near Joshua Tree, California (pers. observ.), while four other fringillids occur there only during winter and spring. Two of these latter (White-crowned and Golden-crowned sparrows) approach or exceed 30 g and have extreme north-south annual migratory patterns, spending summers in far northerly, more mesic locales; the other two (Brewer's Sparrow, 11 g; Sage Sparrow, *A. belli,* 15 g) are xerophilous and migratory to a lesser extent, with winter distributions that include the lower-latitude deserts, and summer distributions shifted northward to include the cooler Great Basin Desert (Chandler

et al. 1966). Thus the seasonal distributional patterns of these birds in the desert seem to shift in a manner that is consistent with size-related constraints on both energy and water balance and with the thermal regimes that they encounter.

In addition to the seasonal patterns in thermal regimes that must influence metabolic regulation of granivorous birds are the 24-hr patterns that, although operating on a different time scale, are nearly equal in amplitude to the seasonal differences, and therefore must correspondingly have an impact on metabolic regulation. These circadian thermal fluctuations are illustrated in Figure 7 for both representative midwinter and midsummer days, and are predictively revealing insofar as daily patterns of water balance are concerned. Aschoff and Pohl (1970) have demonstrated circadian shifts in rates of energy metabolism that are independent of T_a and level of activity; corresponding shifts in EWL have not been rigorously examined but our (MacMillen and Trost 1967) early work on the Inca Dove indicates that circadian shifts in both energy metabolism (and MWP) and EWL occur in parallel, and that the ratio MWP:EWL remains constant at a given temperature whether day or night. Given that assumption, the relationships in Figure 7 predict that during midwinter birds up to 30 g in body mass should be in very favorable states of water balance (i.e., water surplus) during the nocturnal period of colder temperatures, and the 30-g bird that is unable to reduce EWL only briefly experiences a state of water deficit during midday without preformed water intake (hatched area A, Fig. 7); with a reduced rate of EWL the 30-g bird should remain continually in positive water balance. Six months later (midsummer), the warmer thermal conditions are such as to preclude the existence of 30-g birds without substantial preformed water intake, and even the 10-g bird should accrue a water deficit by day without intake of preformed water (cross-hatched area C, Fig. 7), with only the cooler nocturnal temperatures representing a potential period of water surplus. All of these day-active birds are basically incapable of nocturnal activity, and therefore the daylight hours alone provide the window for seeking food and water. The geographic and seasonal distributions of these birds combined with the depictions on Figure 7 predict that, unless a state of water surplus can be achieved overnight (assuming primary dependence upon MWP), the birds will not occur there. This implies further that the water surplus overnight may well be applied to help meet the water deficit incurred by day.

At the time of this writing I am applying this model in studies of arid-zone granivorous parrots in South Australia. This will be followed by a similar study of North American fringillids, as indicated in Table 6.

ACKNOWLEDGMENTS

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