

WATER ECONOMY OF GRANIVOROUS BIRDS: CALIFORNIA HOUSE FINCHES¹

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Abstract. A water economy model for granivorous birds has been proposed that assumes equality between exogenous water intake and excretory (fecal + renal) water loss, with the variables of metabolic water production (MWP) and evaporative water loss (EWL) representing the determinants of states of water balance. The model further states that for each species employing seeds as the primary foodstuff, some ambient temperature (T_a) exists at and below which $MWP \geq EWL$, and positive water balance is achieved. We tested this model with California coastal and desert populations of House Finches (*Carpodacus mexicanus*), both of which conform to the model, but the desert forms invariably are more economical in water regulation than are the coastal forms. We also compared both populations while fully hydrated and while subsisting on minimal water rations (dehydrated), and during both daytime and night-time. Under these treatments the gradient of water economy from most to least economical is night-time/dehydrated > night-time/hydrated > daytime/dehydrated > daytime/hydrated. Ecologically, our studies confirm that House Finches under most circumstances are dependent upon exogenous water supplies; although more economical, the desert forms approach water independence only during the night, when the T_a at $MWP = EWL$ in hydrated birds is 4.9°C and that for dehydrated birds is 11.5°C. These temperatures are frequently encountered in their desert habitat during winter nights.

Key words: *Carpodacus mexicanus*, evaporative water loss, House Finches, metabolic water production, water economy model.

INTRODUCTION

Granivorous endotherms have attracted broad interest, due to the not uncommon capacity of small desert species to maintain body mass on a dry-seed diet, without drinking water (Bartholomew 1972, MacMillen 1972). Prompted by the synthetic reviews of Bartholomew (1972) and Dawson (1976) on water regulation in arid-zone birds, MacMillen and Hinds (1983) and MacMillen (1990) proposed, successively, scaling models to explain and predict states of water balance in heteromyid rodents and granivorous birds, respectively. The avian model (MacMillen 1990) is based in part upon the observed phenomenon that, in the few granivorous birds for which detailed water budget data exist while maintaining body mass in the laboratory, either on a minimal water ration or deprived of drinking water, preformed water intake including that drunk and/or absorbed in the air-dry seed diet approximates excretory (fecal + renal) water

loss. This model also predicts that, for each species, some ambient temperature (T_a) exists at which the other two factors in the water budget equation, metabolic water production (MWP) and evaporative water loss (EWL), become equal, and therefore positive water balance is attained ($MWP/EWL = 1.0$). Thus, states of water balance may be estimated with reasonable accuracy with routine simultaneous measurements of MWP and EWL. Both the avian and mammalian models further state that this temperature of equality (T_a at $MWP = EWL$) is negatively related to body mass, with smaller species attaining more favorable states of water balance than larger ones at the same T_a .

The initial, more simplistic model proved very robust when applied to heteromyid rodents (MacMillen and Hinds 1983). MacMillen's (1990) more refined avian model took into account known metabolic differences between birds that were hydrated vs. those that were dehydrated. This granivorous bird model also proved very robust when applied to Australian granivorous parrots across a broad range in body

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mass (27–391 g), except this application demonstrated that the model required additional allowances for circadian differences in metabolic performance (MacMillen and Baudinette 1993).

Herein we apply the MacMillen (1990) model of water economy in granivorous birds to California coastal and desert populations of the House Finch (*Carpodacus mexicanus*), acknowledging the differences in EWL that were likely to exist between birds that occupy these different habitats (Williams 1996). In addition, this application explores further the extent of expected differences in water balance that are driven by hydration state and circadian influences, as demonstrated in Australian parrots by MacMillen and Baudinette (1993).

METHODS

House Finches were selected for these experiments because of their broad habitat distribution in California; while primarily granivorous, they are secondarily and opportunistically frugivorous (Dawson 1923). House Finches were collected with mist nets and walk-in traps, under California Department of Fish and Game Scientific Collector's Permit No. 1152, about three weeks prior to commencing measurements. The desert birds were collected in the southern Mojave Desert, about 15 km W of Joshua Tree, San Bernardino County, during June 1990. The coastal House Finches were collected in June 1991 in South Laguna, Orange County. Individuals were weighed in the field upon capture and were taken to the laboratory (University of California, Irvine) within a day of capture. They were housed individually in small aviary cages inside an animal room with a stable T_a of about 24°C and a 12-hr photoperiod (lights on 06:00–18:00). Relative humidity of the room, as indicated by an Abbeon Certified Hygrometer, varied between 40 and 60% during the periods of measurements (July 1990 and July 1991). Except during the actual measurements, birds were provided with millet seed ad libitum as their sole food source, and, with the exception of the experiments that dealt with minimal water requirements (hereinafter referred to as dehydrated birds), they were provided with tap water ad libitum (hereinafter referred to as hydrated birds). Different individual birds from each collecting locality were employed in the experiments that dealt with hydrated birds and with dehydrated birds, respectively. All birds were maintained in

compliance with requirements of the University of California, Irvine Animal Research Committee (ARC Permit No. 90-1085).

After several days of body mass maintenance or gain on ad libitum water, four birds of each sex from each collecting locality were placed on daily water rations predetermined to result in positive water balance: coastal finches were placed initially on rations of 2.0 mL day⁻¹ (10.5% body mass day⁻¹), whereas desert birds were placed initially on rations of 1.0 mL day⁻¹ (5.6% body mass day⁻¹). These rations, then, were reduced gradually over several days to the minimum daily water ration for dehydrated birds: that amount required just to maintain a constant body mass, albeit typically reduced somewhat below the ad libitum mass; on less water individuals could not maintain mass. Individuals were weighed (± 0.1 g) at about the same time each morning just prior to watering. The daily water allotment (± 0.1 mL) was delivered with a hypodermic syringe into small conical cups, which were emptied by the birds almost immediately, precluding measurable loss by evaporation.

Rates of oxygen consumption were measured with an Applied Electrochemistry oxygen analyzer (Ametek S-3A) in individual birds held in separate respirometry chambers in a darkened constant temperature chamber. The respirometry chambers were fashioned from 2.0 L clear-glass food storage jars with resealable air-tight lids equipped with three ports, one each for the introduction and exit of air, and for a thermocouple for monitoring chamber temperature. During measurement each bird rested on a wire-mesh floor above a layer of mineral oil into which excreta fell, eliminating it as a source of water vapor. Four chambers, for three birds and a control, were employed simultaneously during measurements; air passing through the empty chamber represented the oxygen concentration and water vapor content of the incurrent air to the chambers.

Incurrent air was dried by flowing it through two columns of indicating Drierite prior to metering it through rotameters into individual chambers at 1 L min⁻¹. The rotameters were calibrated frequently by timing the movement of a soap bubble through a glass cylinder of known volume. The water vapor content of the air inside the chambers was comparable to exceedingly dry desert conditions with the average at

each of the three ambient temperatures used being as follows: $\sim 5^{\circ}\text{C}$, 18%; $\sim 15^{\circ}\text{C}$, 10%; $\sim 25^{\circ}\text{C}$, 5% (after Lasiewski et al. 1966). Excurrent air from the chambers was dried again by passage through Drierite (also used to measure EWL), after which a small subsample from each excurrent airstream was scrubbed of CO_2 with Ascarite, and then directed into the oxygen analyzer.

Calculations of rates of oxygen consumption followed the method of Depocas and Hart (1957) using a RQ of 1, and were corrected to STPD. Because we wished to translate oxygen consumption into metabolic water production while the birds were oxidizing millet, no attempt was made to render the birds postabsorptive and we have assumed they were not (see below). Oxygen consumption determinations were made at 5-min intervals over 40 min, after at least 1 hr of equilibration to the experimental conditions. The resultant eight measurements for each bird were averaged and used to estimate metabolic water production by employing the constant of 1.0 mL O_2 consumed, yields 0.62 mg of metabolic water. This factor is based upon the oxidation of millet (13.5% protein, 5.1% lipid, 81.4% carbohydrate), and the oxygen consumption constants for these foodstuffs (Schmidt-Nielsen 1964, MacMillen and Hinds 1983).

EWL was measured for each individual and at each T_a simultaneously with measures of oxygen consumption to provide concurrent ratios of MWP to EWL. Rates of EWL were determined gravimetrically by flowing excurrent air from each respirometry chamber through U-tubes filled with indicating Drierite, and measuring the mass increase with a precision analytical balance ($\pm 0.0001\text{g}$) for the same period of time (~ 40 min) over which O_2 consumption and MWP were determined. Any water found in the excurrent air from the control chamber was used to correct the values from the birds. The gravimetric method is known to provide an accurate estimate of EWL (Dawson and Fisher 1969), and has been used repeatedly for birds and mammals (MacMillen and Hinds 1983, MacMillen and Baudinette 1993).

Body temperature (T_b) and chamber temperature (T_a) were measured using copper-constantan thermocouples attached to a Yellow Springs Instruments potentiometer. The measurements of T_b , taken at a depth of 1 cm in the cloaca, were completed within seconds after removal of the

bird from its chamber at the end of a respirometry experiment. T_a was measured for each bird at each 5-min interval of O_2 consumption over the 40-min period, with the mean of the resultant eight measurements representing the T_a for that period.

Measurements were made within the ranges of $T_a = 4$ to 10, 13 to 16, and 24 to 26°C , this latter range being within thermal neutrality and the former two ranges below thermal neutrality (Dawson, et al. 1985). Daytime measurements were made between 10:00 and 16:00 after allowing each bird at least 1 hr of equilibration in its chamber; the birds had free access to millet for at least 2 hr prior to placement in respirometry chambers and were presumed to be in non-post-absorptive digestive states. The birds intended for night-time measurements also were allowed free access to millet on the day of measurement, and they typically fed actively during the two afternoon hours prior to placement in respirometry chambers. When birds were placed in the chambers, their crops were usually at least partially full, and the birds were presumed to be in the same non-postabsorptive state during measurement as the daytime birds. Night-time birds were typically placed in chambers between 17:00 and 18:00, and measurements were made 4–5 hr later, between 21:00 and 23:00. Each bird was weighed (± 0.1 g) prior to placement in the chamber and immediately following removal; body mass at the time of measurement was estimated by interpolation. No bird was measured at more than one T_a each day or at night. Usually two groups of three birds each were measured during a single day, and one group of three birds at night. Generally, the duration between the first and last measurement of an individual did not exceed six days. We attempted to use six birds, three of each sex, for each temperature for the day and night measurement within a given hydration state; completely different birds were used in the hydration and dehydration treatments. Occasionally, if available, additional birds were substituted when an individual appeared to be stressed by the experimental protocol; substitutes had received identical experimental treatment simultaneous with the originals. In total we made measurements upon 28 birds broken into the four groups: Coast: hydrated, $n = 8$, dehydrated, $n = 8$; Desert: hydrated, $n = 5$, dehydrated, $n = 7$.

Where appropriate, mean values are expressed

TABLE 1. Body masses (g) on the day of collection, and on the first and last days of measurements for hydrated and dehydrated House Finches.

Group	Mean \pm SE	<i>n</i>	Range
All field	19.75 \pm 0.22	36	15.6–23.0
Hydrated, 1st measurements	18.42 \pm 0.40	13	15.1–21.3
Hydrated, last measurements	17.30 \pm 0.47	11	15.1–20.6
Dehydrated, 1st measurements	16.42 \pm 0.38	15	13.2–19.4
Dehydrated, last measurements	15.36 \pm 0.31	12	13.2–17.6

with their standard errors. Stepwise multiple regression, determined by the method of least squares, was used to determine the importance and relative contributions of various factors (listed below) while interacting with the physiological variables of: oxygen consumption $\dot{V}O_2$, mL O_2 hr⁻¹, evaporative water loss (EWL, mg H₂O hr⁻¹), body temperature (T_b , °C), body mass (m, g), and minimum water requirement (mL H₂O day⁻¹, % m day⁻¹). Factors include continuous ones of ambient air temperature (T_a) and body mass. Other factors were entered into the regressions as dummy variables which were randomly assigned discontinuous values of either 0 or 1 (Kleinbaum and Kupper 1978). These factors include sex (male = 0, female = 1), measurement time of day (DN, night = 0, day = 1), hydration state (HS, hydrated = 0, dehydrated = 1), and collection locality (CD, coastal = 0, desert = 1). Interactions between T_a and mass, and between the continuous and discontinuous factors also were evaluated (e.g., T_a vs. DN).

Only factors with a statistically significant effect (*t*-test with $P < 0.05$) are reported in the regression equations. Significant factors are presented in their order of importance toward explaining variance in the dependent variable: i.e., in the multiple regression equation, $Y = a + b_1(F_1) - b_2(F_2) + b_3(F_1 \times F_3)$, the first factor presented (F_1) is the most important (explains more of the variance) followed by F_2 (the next most important), and the third term (the interaction between F_1 and F_3) is the least important (although significant). Standard errors are reported for these equations, and include those for regression (S_{y_x}), the *y*-intercept (S_a), and each of the coefficients (e.g., S_{b_1} , etc.). Coefficients of determination (r^2) are reported as percentages for each significant factor and for the equation as a whole. The % r^2 of any further factor provides the additional percentage of variability explained by that factor when it is included in the model; it cannot be said that the factor explains

this particular percentage of the variability in and by itself.

RESULTS

BODY MASS

Neither sex nor the collecting locality significantly affected body mass, coastal and desert birds weighing essentially the same at time of capture (denoted below as "all field") and throughout the experimental period (Table 1). Whereas significant losses in body mass were noted at each stage of the experimental period (when compared to original capture mass), the greatest reductions, as expected, were in birds maintaining weight on minimum water rations (dehydrated; Table 1). In addition, reductions of about 1 g occurred between the first and last day of each experimental procedure, likely attributable to enforced fasting during daytime measurement combined with progressive flight muscle atrophy during confinement in small cages (Table 1).

The relationship between body mass (g) and significant factors affecting it is best described by the multiple regression equation of

$$\text{mass} = 18.4 - 1.98\text{HS} + 1.35\text{PE} - 1.08\text{Ms},$$

$$n = 87 \text{ (28 birds)}, \quad r^2 = 0.61,$$

where HS = hydration state; PE = prior to experimental measurement (other than "all field" group = 0; all field = 1); Ms = day of measurement (1st day = 0, last day = 1). The stepwise regression analysis indicates that 61% of the variation in body mass can be explained by the three factors, in order of decreasing importance: hydration state (45%), the time from collection to first hydrated measurement (12%), and time between first and last measurement in a given hydration state (4%).

For hydrated birds, the mean \pm SE body mass obtained during the physiological measurements was 17.5 \pm 0.4 g ($n = 13$); for dehydrated birds

TABLE 2. Minimum water requirements of dehydrated coastal and desert House Finches (rations expressed as ml of water per day and percent of body mass per day).

Sample	Mean \pm SE	<i>n</i>	Range
ml water day ⁻¹			
Coast	1.28 \pm 0.06	8	1.0–1.5
Desert	0.54 \pm 0.04	7	0.4–0.6
% m day ⁻¹			
Coast	7.82 \pm 0.50	8	5.49–10.07
Desert	3.25 \pm 0.24	7	2.45–4.14

mean mass was 16.2 \pm 0.4 g (*n* = 15). These body masses are used in all subsequent calculations and comparisons.

MINIMUM WATER REQUIREMENTS

In desert birds, minimum daily water requirements were strikingly and significantly reduced to about one-half those of coastal birds, expressed either in absolute or mass-relative terms (Table 2). Sex of the birds had no effect on minimum water requirements.

OXYGEN CONSUMPTION

Oxygen consumption, and thus metabolic water production, was significantly affected by several factors: one interaction and all but one of the factors employed in the analysis (except sex). These significant factors are itemized in the order of their importance in the multiple regression equation of

$$\begin{aligned} \dot{V}O_2 = & 43.58 - 2.47T_a - 24.69DN + 4.05m \\ & + 5.77CD + 0.54T_a(DN) + 3.87HS, \\ n = & 131 \text{ (28 birds)}, \quad r^2 = 0.83, \end{aligned}$$

where T_a = ambient air temperature, DN = measurement time (day = 0, night = 1), *m* = mass (g), CD = habitat, and HS = hydration state. The combined factors explain 83% of the total variation in oxygen consumption, with ambient temperature (60%), time of day (14%), body mass (5%), and collection locality (2%) being the most important contributors (81 out of 83%). Hydration state contributed the least of those features (< 1%) considered, with the interaction between T_a and time of day being only slightly greater (1%) (Fig. 1A). The role of body mass in this analysis is somewhat misleading as the data are expressed in absolute terms (mL O₂ hr⁻¹); when expressed in mass-relative terms

(mL O₂ g⁻¹ hr⁻¹), body mass has no significant effect.

The most important features in the patterns of $\dot{V}O_2$ (Fig. 1A) include significant reductions of 25% in night-time birds compared to daytime birds. Conversely, significantly higher rates of $\dot{V}O_2$ (and hence MWP) occurred in both hydrated and dehydrated desert birds compared to coastal birds. These differences range from 6% at 5°C to 12% at 25°C. Dehydrated birds of both desert and coastal populations also had significantly higher metabolic rates than did hydrated birds (4–8% across the temperature range). It is important to note that these comparisons are valid only for animals of the same body mass. Because the dehydrated birds have a lower body mass (16.2 g), their oxygen consumption appears slightly lower than the larger hydrated birds (17.5 g) in Fig. 1A.

EVAPORATIVE WATER LOSS

The relationship of evaporative water loss and significant factors affecting it are best described by the multiple regression equation of

$$\begin{aligned} EWL = & 108.01 - 35.67DN - 16.95HS \\ & - 15.03CD, \\ n = & 131 \text{ (28 birds)}, \quad r^2 = 0.51, \end{aligned}$$

where DN = measurement time, HS = hydration state, and CD = habitat. Time of day (35%), hydration state (10%), and collecting locality (6%) significantly affected rates of evaporative water loss, combining to account for 51% of the observed variation. These effects are most apparent in Figure 1B, which reveals that: (1) EWL is independent of T_a from 5–25°C as expected, (2) in any one experimental treatment, EWL of coastal birds exceeds that of desert birds, (3) night-time rates of EWL are considerably lower than daytime rates, and (4) EWL of dehydrated birds is significantly lower than in hydrated birds. Sex had no observed effect on EWL.

RATIO OF METABOLIC WATER PRODUCTION TO EVAPORATIVE WATER LOSS (MWP/EWL)

The factors that significantly affect MWP/EWL when interacting with body mass are ambient temperature (24%), collecting locality (12%), time of day (10%), and hydration state (5%), combining to explain 51% of the variation.

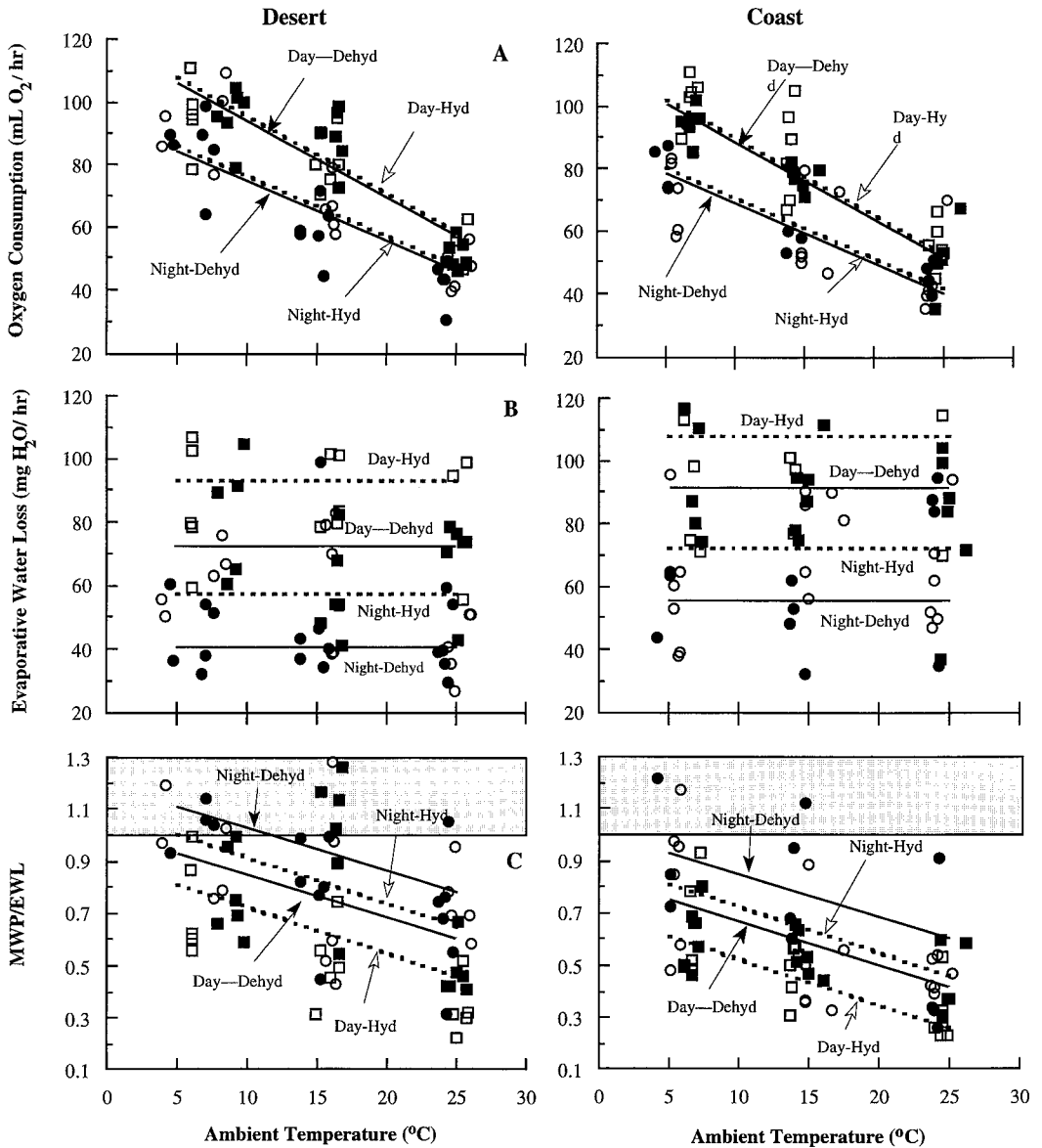


FIGURE 1. Relationship of oxygen consumption (A, top), evaporative water loss (B, middle), and ratio of metabolic water production to evaporative water loss (C, bottom) to ambient air temperature in desert (left) and coastal (right) House Finches. Symbols: rectangles, day; circles, night; filled symbols, dehydrated; open symbols, hydrated. Hydrated (dashed lines) and dehydrated birds (solid lines) were measured during daytime and nighttime. Lines are based on equations given in the text, and each line differs significantly from all others for that variable (dehydrated desert birds measured in the day differ from the other three experimental groups of desert birds, and from their coastal counterparts). Body mass significantly affected oxygen consumption (A) and MWP/EWL (C); therefore, 17.5 and 16.2 g for hydrated and dehydrated birds, respectively, were used to calculate the lines for these two variables. The shaded area in C indicates positive water balance, where metabolic water production equals or exceeds evaporative water loss.

TABLE 3. T_a at MWP = EWL in coastal and desert House Finches and in the Australian desert Budgerigar (*Melopsittacus undulatus*)^a.

Species and locality	Mass (g)	T_a at MWP = EWL (°C)			
		Hydrated		Dehydrated	
		Night	Day	Night	Day
Coastal House Finch	17	-6.1	-17.1	0.5	-10.5
Desert House Finch	17	4.9	6.1	11.5	0.5
Australian Budgerigar	27	18.0	10.8	18.2	13.3

^a MacMillen and Baudinette 1993.

These relationships are best described by the multiple regression equation of

$$\begin{aligned} \text{MWP/EWL} = & 0.70 - 0.001m(T_a) \\ & + 0.011m(\text{CD}) + 0.011m(\text{DN}) \\ & + 0.008m(\text{HS}), \\ n = & 131 \text{ (28 birds)}, \quad r^2 = 0.50, \end{aligned}$$

where m = mass (g), T_a = ambient air temperature, CD = habitat, DN = measurement time, and HS = hydration state. Sex and body mass as single factors were unimportant contributors to the observed variation.

Figure 1C reveals separately for desert and coastal birds the relationships between MWP/EWL and T_a for each of the experimental treatments. In these relationships the regression slopes are negative and parallel as anticipated, and desert birds have higher values at any one T_a than do coastal birds (i.e., desert birds have more favorable states of water balance than coastal birds). At any one T_a , the most favorable states of water balance in birds from either locality are observed in night-time/dehydrated samples, followed by night-time/hydrated birds, then daytime/dehydrated ones, and lastly daytime/hydrated birds. These differences translate into considerable differences in the T_a at MWP = EWL, with desert birds in each treatment having temperatures at which water balance is achieved about 10°C higher than in coastal birds (Fig. 1C, Table 3).

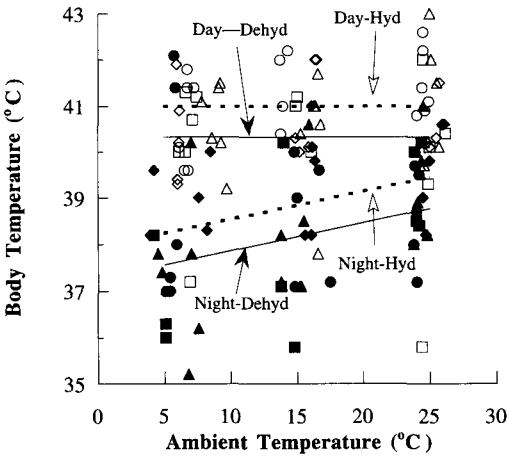


FIGURE 2. The relationship of body temperature to ambient air temperature of coastal and desert House Finches. Symbols: filled, night; open, day; circles, coast, hydrated; squares, coast, dehydrated; diamonds, desert, hydrated; triangles, desert, dehydrated. Birds were measured during daytime and night-time while hydrated (dashed lines) or dehydrated (solid lines). Lines are based on the equation for T_b given in the text, and each line differs significantly from the others. Hydrated birds of either coastal and desert population had higher T_b during day than at night. The higher daytime T_b s did not change with T_a , whereas night-time T_b s increased with increasing T_a .

BODY TEMPERATURE (T_b)

The factors that significantly affected T_b in these experiments (and their percentile contributions) were time of day (37%), hydration state (4%), and the interaction between T_a and time of day (3%), combining to explain 44% of the observed variation. These relationships are best described by the multiple regression equation of

$$\begin{aligned} T_b = & 41.0 - 3.05\text{DN} - 0.68\text{HS} + 0.06T_a(\text{DN}), \\ n = & 83 \text{ (28 birds)}, \quad r^2 = 0.44, \end{aligned}$$

where DN = measurement time, HS = hydration state, and T_a = ambient air temperature. Neither sex, body mass, nor collecting locality were significant contributors to this variation

Because T_b was independent of sex, body mass, and collecting locality, the data were pooled for regression analysis, to show relationships between T_b and T_a measured by day and night, and in hydrated and dehydrated birds (Fig. 2). This analysis reveals that during the daytime,

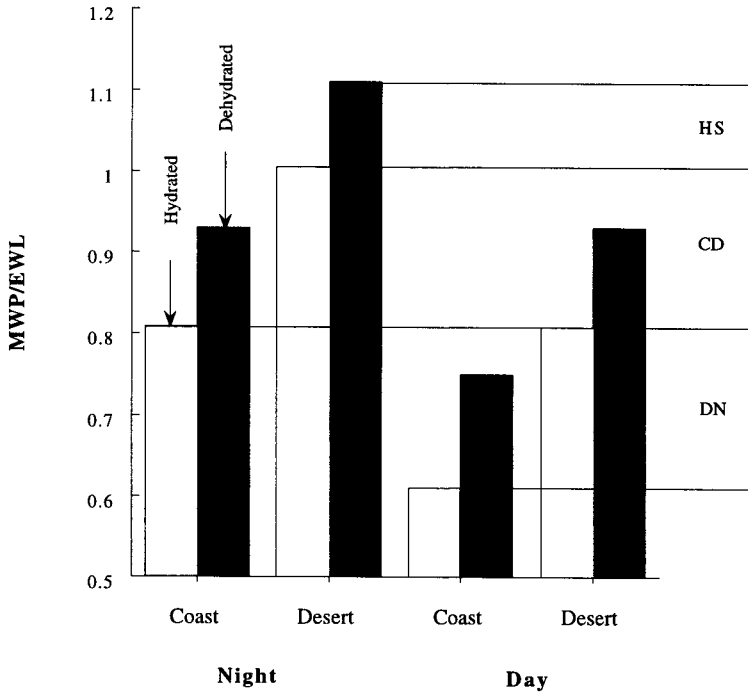


FIGURE 3. Ratio of metabolic water production to evaporative water loss (MWP/EWL) at an ambient temperature of 5°C of coastal and desert House Finches. Birds were hydrated (light bars) or dehydrated (dark bars) and measured at night-time or daytime. MWP/EWL are those predicted by the appropriate equation in the text for birds of a body mass of 16.2 g (dehydrated) or 17.5 g (hydrated). The effects upon MWP/EWL of hydration state (HS, hydrated vs. dehydrated), time of measurement (DN, day vs. night), and collection locality (CD, coastal vs. desert) are indicated by representative horizontal lines with labels to the right. For example, for hydration state (HS), the dehydrated birds have a higher ratio by 0.1 than hydrated ones regardless of time of measurement and collection locality; this is indicated by the horizontal lines drawn to the night-time, desert set of bars.

T_b was independent of T_a , but that hydrated birds had significantly higher T_b s than dehydrated birds. In contrast, during the night-time T_b was significantly and positively related to T_a , all night-time T_b s were significantly reduced below daytime values, and night-time, dehydrated birds had T_b s that were significantly reduced below those of night-time hydrated birds (Fig. 2). Therefore, depending upon the experimental treatment, T_b varied from a low of about 37°C (night-time dehydrated birds at $T_a = 5^\circ\text{C}$) to a high of about 41°C (daytime hydrated birds at T_a s of 5–25°C), showing considerable lability under these environmental influences (Fig. 2).

DISCUSSION

The MacMillen (1990) model of water economy in granivorous birds accounts for mass-related differences within an avian taxon as well as the effects of hydration state. In this study of the

House Finch, a single species of nearly uniform mass, we again confirm the effect of hydration state on the water economy of granivorous birds (see also MacMillen and Baudinette 1993). In addition, we extended the model to include the roles in water economy of the discontinuous variables of time of day (i.e., day or night), and collecting locality (i.e., coastal or desert). In every respect House Finch performances conformed to model expectations, with $\dot{V}O_2$ (and MWP) negatively related to T_a , and EWL independent of T_a ; consequently, the ratio MWP/EWL also was negatively related to T_a (Fig. 1). In addition, the discontinuous variables of hydration state, time of day, and collecting locality each significantly affected the components of water economy that we examined (Fig. 3); these factors interacted to yield a gradient of states of water economy.

These states of water economy may be iden-

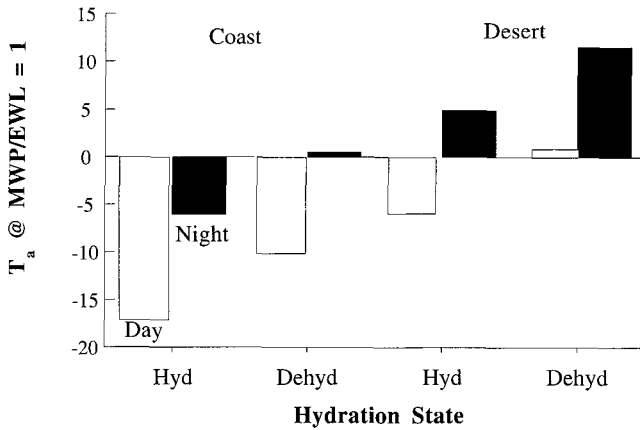


FIGURE 4. The ambient air temperature at which metabolic water production equals evaporative water loss (T_a at $MWP = EWL$) in coastal and desert House Finches. Birds were measured at night-time (dark bars) or daytime (light bars) in either the hydrated (Hyd) or dehydrated (Dehyd) state. The T_a at $MWP = EWL$ is higher in desert birds and increases during night-time and in the dehydrated state.

tified either by the magnitude of MWP/EWL at any one T_a (Fig. 3), or its derivative, T_a at $MWP = EWL$ (the T_a at which water balance is achieved; Fig. 4, Table 3). Within the sample of House Finches from a given collecting locality, the gradient in water economy, from most to least economical, follows the pattern: night-time, dehydrated > night-time, hydrated > daytime, dehydrated > daytime, hydrated. Invariably, desert House Finches were markedly more economical than were coastal ones while exposed to any one set of hydration state + time of day (Fig. 4, Table 3). It also is interesting to note that desert House Finches, in either hydrated or dehydrated states, had rates of oxygen consumption (and therefore MWP) that were significantly elevated over their coastal counterparts (Fig. 1). Furthermore, both desert and coastal finches, when dehydrated, had significantly elevated rates of oxygen consumption (and MWP) than when hydrated (Fig. 1). These data suggest that intensity of energy metabolism (and MWP) is sensitive to water regulatory demands.

Differences in physiological parameters between geographically separated House Finch populations have been noted before, with suggestions that some of these differences may have developed over evolutionarily brief periods of time (e.g., less than 100 years; O'Connor 1996). Williams (1996), in a recent survey of avian EWL , has demonstrated across a broad taxonomic scale that birds from arid environments have statistically lower rates of evaporative wa-

ter loss than do their mesic-inhabiting counterparts. Nevertheless, the substantial differences in water economy we have noted between coastal and desert races of House Finches in California were quite surprising, particularly because the two collecting localities are only about 166 km apart in linear distance. However, the elevational gradient between the two localities is very substantial, with three mountain ranges lying between the coastal and desert collecting localities, respectively: the Santa Ana Mountains (maximum elevation, 1,737 m), the San Jacinto Mountains (max. 3,292 m), and the Little San Bernardino Mountains (max. 1,890 m). Each of these ranges contributes successively to a rain-shadow effect resulting in progressive aridity, and collectively they also may serve as genetic barriers, effectively isolating the two House Finch populations and promoting the physiological divergences we found.

When placed in an ecological context, these interpopulational differences make sense, with the coastal population inhabiting a climatically moderate, urban setting where surface water abounds throughout the year. In contrast, the desert population inhabits a region of sparse winter rainfall, and hot, dry summers, with unreliable and distant sources of natural surface water. Because all of our measurements were made on birds adjusted to summer conditions, we are unable to state whether there are seasonal differences in performance of the parameters we measured. Assuming there are not, and with

midsummer temperatures at the desert collecting locality (July; MacMillen 1990) varying over 24 hr between ca. 22 and 39°C, even the desert House Finches are continually threatened with states of negative water balance (MWP < EWL), unless drinking water or succulent foods are nearly continuously available. These summer periods must limit their existence to localities within short flight distances to water. However, during midwinter, the same desert locality, with its intermediate elevation of about 1,000 m, yields 24-hr ambient temperatures that may vary between -5 and 15°C (January; MacMillen 1990). These temperatures provide nocturnal conditions during which MWP may exceed EWL, resulting in at least nocturnal accrual of positive water balance; winter daytime temperatures, however, would seem to demand reliance upon an exogenous water source (Table 3).

Despite the differences in water economy between these coastal and desert populations of House Finches, we are not inferring that either comes close to water independence as has been suggested for certain other small granivorous birds (MacMillen 1990). Rather, we are stating that House Finches conform nicely to the predictions of the MacMillen model (1990), and that there are demonstrable differences between coastal and desert populations, with the latter being more efficient in water regulation consistent with the physical conditions of its habitat. In addition, House Finches from either habitat are able to improve their water regulatory efficiencies through adjustments in response both to temporal (night vs. day) and hydration (dehydrated vs. hydrated) states. Perhaps these adjustments, as suggested by Webster and Bernstein (1987), result from changes in water permeability of the skin that promote varying levels of water vapor diffusion resistance. This contention is strengthened by the findings of Menon et al. (1989) who have shown that Zebra Finches (*Poephila guttata*) under water stress are able to reduce cutaneous water loss by altering the lipid composition of the skin. Whatever these adjustments may be, it is apparent from both this study and our earlier study of Australian parrots (MacMillen and Baudinette 1993) that the adjustments may be both rapid and reversible, promoting repeated circadian changes in water economy.

At present there are far too few data of the nature we report to allow taxonomically-valid

comparisons among granivorous birds. However, our data (this paper, and MacMillen and Baudinette 1993) suggest that Australian desert parrots may be considerably more efficient in water regulation than American fringillids, as implied in Table 3, particularly when allowances for mass differences are made. Table 3 reveals that a 27 g Budgerigar achieves positive water balance (MWP = EWL) at T_{1s} about 10°C higher, under all experimental conditions, than does a desert House Finch of 17 g. Further taxonomic comparisons cannot be made until fringillids and other granivorous avian taxa are examined across broader size ranges, as in our Australian parrots. We invite such examinations for further clarification.

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