

ENERGETICS AND WATER BALANCE IN FREE-LIVING TROPICAL HUMMINGBIRDS¹

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Abstract. In Costa Rica's humid, Caribbean lowlands, we used the doubly-labeled water (DLW) technique to measure field metabolic rate (FMR) and water influx of free-living Crowned Woodnymphs (*Thalurania colombica*) (mean mass = 4.90 g) and Bronze-tailed Plumeleteers (*Chalybura urochrysis*) (mean mass = 7.23 g). FMR averaged 37.9 kJ/day in woodnymphs ($n = 9$) and was 57.9 kJ/day in a single plumeleteer. The former value is 26% higher than expected from the birds' mass, based on other DLW studies. Water influx averaged 2,392 ml/(kg·day) in woodnymphs ($n = 12$) and 2,001 ml/(kg·day) in plumeleteers ($n = 2$). These are the highest water flux rates measured for any bird and are equivalent to turning over, respectively, 366% and 304% of the birds' total body water content each day.

Key words: Tropics; hummingbird energetics; field metabolic rate; doubly-labeled water; water flux.

INTRODUCTION

Over the past decade, more than a score of studies have used the doubly-labeled water (DLW) technique to quantify the field metabolic rate (FMR) and water flux rate of free-living birds (see Nagy 1987). Although these studies reveal that the FMR of desert birds is lower than that of nondesert birds, and that seabirds differ from nonseabirds (Nagy 1987), more data are needed to fully appreciate how environmental and life history traits influence the water and energy budgets of wild birds. Studies of tropical landbirds seem especially desirable both because the tropics are being rapidly modified by human activities and because the majority of bird species reside in the tropics.

Laboratory studies have revealed that some lowland tropical landbirds have comparatively low basal metabolic rates (BMR) (Weathers 1977, 1979, 1986). The following considerations suggest that they may also have low FMR. Lowland tropical birds tend to be less active than temperate species, and their activity is restricted to about a 12-hr day. In contrast, temperate and arctic birds experience 15–24 hr of daylight during the breeding season. Consequently, during the summer, lowland tropical birds should spend a greater proportion of the 24-hr day resting than

would birds that reside at high latitudes. Furthermore, the warm temperatures typical of the lowland tropics might reduce thermoregulatory requirements. Because basal plus thermoregulatory costs are thought to account for 40–80% of a bird's total energy costs (Walsberg 1983), lowland tropical species might require substantially less energy than temperate or arctic species.

Despite the above considerations, no studies have directly determined the FMR of tropical landbirds. Thus, to increase our understanding of tropical bird energetics, while simultaneously expanding our knowledge of the world's smallest birds, we used the DLW technique to measure the water and energy relations of two lowland, tropical hummingbird species.

MATERIALS AND METHODS

STUDY AREA AND SPECIES

Our study was conducted during 2–4 July 1985 at Finca La Selva, a biological station operated by the Organization for Tropical Studies, which is situated at an elevation of about 75 m in the Atlantic lowlands of NE Costa Rica about 2.5 km SW of the town of Puerto Viejo de Sarapiquí (10°26'N, 84°1'W). The mean daily air temperature at La Selva averages 24°C, with little seasonal variation; mean annual rainfall is about 4 m, with the wettest months being July and December (cf. Stiles 1975).

We measured FMR and water flux rate of free-

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living male Crowned Woodnymphs (*Thalurania colombica*) and Bronze-tailed Plumeleteers (*Chalybura urochrysis*). Both species breed at La Selva, but in early July the breeding season had just ended and most of the birds were undergoing their annual molt (Stiles 1980). Most of the males we studied held feeding territories at clumps of *Heliconia imbricata* (Musaceae), a large, cloning, perennial herb with nectar-rich flowers (Stiles 1975). The *Heliconia* clumps were adjacent to an abandoned cacao plantation located on a recent alluvial terrace of the Rio Puerto Viejo. We captured birds between 08:00 and 12:00 with mist nets set near the *Heliconia* clumps, and identified individuals with color-coded acetate leg tags (Stiles and Wolf 1973) that weighed less than 0.1 g, or no more than 1% of the bird's weight.

DOUBLY-LABELED WATER

Doubly-labeled water measurements are difficult to make on hummingbirds because their wings and legs do not provide prominent veins from which blood samples can be easily obtained. Toe clipping only occasionally produces sufficient amounts of blood and attempts to obtain blood from the single, large, prominent, jugular vein usually result in excessive hemorrhaging. To minimize trauma and disturbance to the bird, we therefore employed the single-sample DLW technique (Nagy et al. 1984; Ricklefs and Williams 1984; Obst et al. 1987; Webster and Weathers 1989).

We injected and released 43 birds into the field (nine *Chalybura*, mean mass = 7.23 ± 0.50 g and 34 *Thalurania*, mean mass = 4.90 ± 0.25 g). We recaptured two *Chalybura* and 14 *Thalurania*: 11 of these within approximately 1 day and five within approximately 2 days of their release. One of the 1-day recapture samples was lost in processing and none of the 2-day birds contained sufficient ^{18}O to permit calculation of CO_2 production. For one of the 1-day birds, $^{18}\text{O}_t$ was too low (within 0.0012 atom % of background) to provide reliable estimates of CO_2 production (see Reliability of Data, below). ^3H levels of all but two of the recaptures were sufficient to permit calculation of water flux rates.

Within 5 min of initial capture, hummingbirds were weighed to the nearest 0.05 g with a 10-g Pesola spring balance, given an intramuscular (pectoralis) injection of 15–25 μl of water (containing 95+ atom percent ^{18}O and ca. 0.6 MBq

^3H) with a Hamilton 50- μl syringe, and released. One or 2 days later they were recaptured and reweighed, and a 70- to 100- μl blood sample was obtained by puncturing the jugular vein and filling one or two heparinized hematocrit tubes. The tubes were sealed with Critocaps in the field and taken to the laboratory at La Selva, where they were flame-sealed and stored at 4°C. They were later transported under refrigeration to the University of California, Davis, for processing. Blood samples were microdistilled under vacuum to obtain pure water, which was assayed for tritium activity (Searle model Mark III liquid scintillation counter, toluene-Triton X100-PPO scintillation cocktail) and for oxygen-18 content by cyclotron-generated proton activation of ^{18}O to fluorine-18 with subsequent counting of the positron-emitting ^{18}F in a Packard Gamma-Rotomatic counting system (Wood et al. 1975).

MEASUREMENT OF TBW

Determinations of isotope levels in an initial (postequilibrium) blood sample are typically used in DLW studies to calculate the initial total body water volume (TBW_i) and the initial, background-corrected, isotope ratio ($\ln \text{O}^*/\text{H}^*$) required in the CO_2 production calculations. In this study, initial postequilibrium isotope levels were estimated from a separate control group of eight hummingbirds: three *Chalybura* and five *Thalurania* (for rationale, see Nagy et al. 1984). These birds were captured and injected with DLW as described above, held for 1 hr in the field, weighed, and a blood sample obtained as above. They were then sacrificed, taken to the laboratory, reweighed, and dried to constant mass (determined to the nearest 0.1 mg with a Mettler H30 balance) at 70°C (see Crumb et al. 1985). From the isotope levels in the control blood samples, we calculated the predicted initial isotope ratio (background-corrected) for experimental birds ($\ln ^{18}\text{O}_i/{}^3\text{H}_i = -10.3527 \pm 0.0224$). We used this ratio in our FMR calculations. We regressed the initial tritium activity of the controls against μl DLW injected/g body mass to obtain the following equation, from which we estimated the initial ^3H level for field birds:

$$^3\text{H activity (cpm)} = 4,630X - 470$$

$$(r^2 = 0.952, s_{y,x} = 338.8, s_b = 424.2),$$

where X is the μl of DLW injected per gram body mass. For the control birds, the mean algebraic

TABLE 1. Water and energy relations of free-living tropical hummingbirds.

Bird no.	Body mass		Time, days	Energy		Influx		Water			
	Mean, g	% change/day		ml CO ₂ /g·hr	kJ/day	ml/kg·day	ml/day	Meta-bolic water ml/day	Influx—metabolic ml/day	Diet ml/day	Input from: Drinking ml/day
<i>Thalurania colombica</i>											
13	5.13	-0.97	1.102	14.09	37.29	2,663	13.66	1.15	12.51	8.36	4.15
17	4.98	1.01	1.006	12.46	32.00	2,724	13.57	0.99	12.58	7.17	5.41
24	4.58	1.10	0.949	18.25	43.12	2,963	13.57	1.33	12.24	9.66	2.58
26	4.70	-2.11	0.949	15.03	36.43	2,031	9.55	1.12	8.43	8.16	0.27
33	4.73	3.23	1.036	14.21	34.66	2,169	10.26	1.07	9.19	7.77	1.42
34	5.10	1.98	0.975	10.44	27.47	2,664	13.59	0.85	12.74	6.16	6.58
40	5.18	-0.96	0.930	18.63	49.77	2,155	11.16	1.53	9.63	11.16	-1.53
47	4.98	1.01	0.971	15.72	40.38	2,222	11.07	1.24	9.83	9.05	0.78
48	4.83	-3.06	0.848	16.09	40.08	1,684	8.13	1.23	6.90	8.99	-2.09
\bar{x}	4.91	0.14	0.974	14.99	37.91	2,364	11.62	1.17	10.45	8.50	1.95
SD	0.20	1.92	0.067	2.45	6.11	386	1.96	0.20	2.14	1.45	2.99
<i>Chalybura urochrysa</i>											
22	7.20	-2.74	1.955	—	—	2,028	14.60	—	—	—	—
32	7.18	2.11	0.996	15.64	57.92	1,973	14.17	1.78	12.39	12.99	-0.60

error for $^3\text{H}_i$ predicted by this equation was $1.77 \pm 0.75\%$.

For a constant injection volume, the relation between $^3\text{H}_i$ specific activity (cpm) and milliliters of dilution volume (which is a function of body mass) is a curve, described by the equation $C = XY$, where $Y = \text{cpm}$, $X = \text{ml TBW}$, and C is a constant (see Nagy 1980). Previous applications of the single sample DLW method (see Webster and Weathers 1989) have used the $^3\text{H}_i$ activity and TBW_i of controls to calculate a constant, C_H , from the equation $C_H = ^3\text{H}_i \times (\text{TBW}_i [\text{ml}])$. This constant and an estimate of TBW_i is used to calculate the initial $^3\text{H}_i$ of experimental animals. Theoretically this approach should give more accurate estimates of $^3\text{H}_i$ than the linear approximation which we used above. However, for our control birds, in which different injection volumes were used for the two species, the linear approximation yielded marginally better results. Mean C_H values calculated as above for our control birds were 44,368 cpm·ml for *Thalurania* ($n = 5$) and 70,915 cpm·ml for *Chalybura* ($n = 3$). Coefficients of variation for C_H were 1.31% and 4.53%, respectively. For our control birds, the mean algebraic error of predicted $^3\text{H}_i$ (compared to the measured H_i) calculated by dividing C_H by TBW_i was $1.85 \pm 1.74\%$. The corresponding error for linear approximation was slightly smaller and significantly less variable ($1.77 \pm 0.75\%$; $F = 5.4$, $P < 0.05$). The linear approximation provided a somewhat better estimate for our control birds

for two reasons. First, because different injection volumes of DLW were used for the two species, the sample size from which C_H was calculated was small for both species. Sample size was effectively increased by using a linear approximation which regresses $^3\text{H}_i$ against $\mu\text{l DLW}$ injected/g body mass. Second, although the relation between $^3\text{H}_i$ activity (cpm) and milliliters of dilution volume is a curve, the arc of the curve is so shallow that over a fairly broad range of TBW a straight line adequately describes the data. For *Thalurania*, mean water influx calculated using C_H to estimate $^3\text{H}_i$ was $2,367 \pm 413 \text{ ml kg}^{-1} \cdot \text{day}^{-1}$. Mean water influx based on the linear approximation was 0.13% lower, $2,364 \pm 386 \text{ ml kg}^{-1} \cdot \text{day}^{-1}$ (Table 1).

We determined the final total body water content (TBW_f) of experimental birds by killing them in the field immediately after obtaining the single blood sample and drying them to constant mass at 70°C. The experimental bird's TBW_i was calculated from the bird's initial body mass (M_i) and TBW_i, assuming a constant water proportion. It seemed possible that the bird's plumage might absorb significant amounts of water from the moist tropical air. If so, drying would overestimate TBW. To check this, we carefully plucked a 4.55-g male *Thalurania*, exposed the plucked feathers to the moist ambient air for several hours, weighed them to the nearest 0.1 mg, and then dried them to constant weight at 70°C. The water absorbed by the plumage equaled 0.387% of the bird's fresh body weight. TBW_f of

control birds determined by drying (corrected for plumage water content) averaged $0.676 M_i \pm 0.020$, and was $102.4 \pm 5.5\%$ of the value calculated from ^{18}O dilution. The TBW of experimental birds was likewise corrected for plumage water content.

We calculated CO_2 production, $\text{ml}/(\text{g}\cdot\text{hr})$, from the ^3H and ^{18}O levels (corrected for background concentrations) by the following equation:

$$\left[\frac{51.86(\text{TBW}_f - \text{TBW}_i)}{(M_i + M_f) \ln(\text{TBW}_f/\text{TBW}_i) t} \right] \cdot \left[\ln \frac{O_i}{H_i} - \ln \frac{O_f}{H_f} \right]$$

where TBW is total body water, M is body mass, and t is the interval in days between 1 hr after isotope injection and the time that the single blood sample was taken.

ENERGY EQUIVALENT OF CO_2 PRODUCTION

Converting field metabolic rates from CO_2 production to units of energy requires knowledge of the bird's diet. Although our hummingbirds fed mostly on *Heliconia imbricata* nectar, they also caught insects sporadically throughout the day. Flycatching attempts occurred more during warm, sunny periods than during cool, shady ones because small insects were more active then. Hummingbirds often spent the first 1–2 hr of the day in the forest canopy catching insects and the first birds captured during the day typically had insects in their crops. The total time spent insect catching averages about 15–25% of that spent foraging for nectar (Stiles, unpubl. data). The amount of energy obtained from insects is probably lower than that predicted from the proportion of time spent insect catching, however, as some insects undoubtedly elude the fly-catching attempts. Therefore, we assumed that the hummingbirds' diet consisted of 90% nectar and 10% insects. *Heliconia imbricata* nectar consists virtually entirely of sugar and water and thus has a heat equivalent for CO_2 production of 21.1 $\text{kJ}/\text{l CO}_2$ (Carpenter 1948). The heat equivalent of insects was assumed to be 24.6 $\text{kJ}/\text{l CO}_2$ (Williams and Nagy 1985). From these values we estimate that 21.5 kJ of heat were produced per liter CO_2 produced.

WEATHER

Half of our labeled birds (nos. 10–30) were free-living during a rainy period (2–3 July), with rain

between 10:30–11:30 and 13:30–16:30, and with periods of heavy rain overnight. Air temperature during this period ranged from 23.5 to 26°C. The other half (nos. 31–52) were released during a dry period (3–4 July) of generally sunny, clear skies and temperatures between 23.0 and 26°C.

RELIABILITY OF DATA

We can gauge the accuracy of our analytical technique from standards and from the coefficients of variation (CV) for triplicate ^{18}O samples. For the ^3H analysis, the mean algebraic error of standards was 0.42%, and the absolute maximum error in any one measurement was 1.11% ($n = 22$). The mean CV for triplicate ^{18}O samples analyzed with the cyclotron was 0.48%, and the mean algebraic error in six recent analyses of ^{18}O standards was 0.0005 atom % (max. error = 0.0012 atom %).

Because isotopes in our hummingbirds turned over rapidly, $^{18}\text{O}_f$ values were fairly close to background (0.0033 to 0.0224 atom % above background). Ricklefs et al. (1986) found that calculated CO_2 production increased as $^{18}\text{O}_f$ approached background and adjusted their CO_2 calculations using a lower hypothetical background. The CO_2 production of our hummingbirds showed no tendency to increase as $^{18}\text{O}_f$ approached background, however, obviating the need to adjust our values. Even though our $^{18}\text{O}_f$ values are low, we believe the estimates of CO_2 production derived from them to be reliable.

Although we did not validate the single-sample DLW method specifically for hummingbirds, in a subsequent validation of our technique using 6-g Verdins (*Auriparus flaviceps*) (Webster and Weathers 1989), CO_2 production of individuals measured by DLW differed by less than 11% from values determined simultaneously by the Haldane method (mean difference, 0.5%). No direct validation of single-sample DLW method for measuring water flux is available, but the single-sample method provides values that are equivalent to those of the double sample method (Webster and Weathers 1989), for which maximum errors are about 15% (Nagy and Costa 1980). Numerical results are presented as mean \pm one standard deviation.

RESULTS AND DISCUSSION

FIELD METABOLIC RATE

Field metabolic rate (CO_2 production) was 15.64 $\text{ml CO}_2/(\text{g}\cdot\text{hr})$ for the one recaptured *Chalybura*

TABLE 2. Rest phase basal metabolic rate (BMR) and field metabolic rate (FMR) of very small birds.

	Mass, g	n	BMR kJ/day	FMR		FMR/ BMR	Source
				kJ/ day	kJ/ g ^{0.64} ·day		
Nectarivores							
<i>Calypte anna</i>	4.5	8	9.2 ^a	32	12.2	3.5	Powers and Nagy 1988
<i>Thalurania colombica</i>	4.9	9	6.2 ^b	38	13.7	6.2	This study
<i>Chalybura urochrysa</i>	7.2	1	8.3 ^b	58	16.4	7.0	This study
<i>Acanthorhynchus tenuirostris</i>	9.7	6	21.5	53	12.4	2.5	Weathers and Paton, unpubl. data
Frugivore							
<i>Zosterops lateralis</i> ^c	9.5	9	16.3 ^b	43	10.3	2.7	Rooke et al., unpubl. data
Insectivores							
<i>Auriparus flaviceps</i>	6.6	11	13.4	30	9.0	2.2	Webster and Weathers, unpubl. data
<i>Malurus cyaneus</i>	8.2	2	14.7 ^b	34	8.8	2.3	Weathers and Paton, unpubl. data
Granivore							
<i>Estrilda troglodytes</i> ^d	6.7	9	11.4	57	16.9	5.0	Weathers and Nagy 1984

^a Calculated by reducing active phase value (12.4 kJ/day; Powers, unpubl. data) by 25%.

^b Predicted value (Aschoff and Pohl 1970).

^c Feeding in grape vineyard at time of study.

^d Captive birds in large flight aviary.

and averaged 14.99 ml CO₂/(g·hr) for the nine *Thalurania* (Table 1). From these values, we estimate that daily energy expenditure was 57.9 kJ/day for the one *Chalybura* and averaged 37.9 kJ/day for *Thalurania*.

Comparing our tropical hummingbirds' FMR with that of other very small birds is complicated due to interspecific differences in body size and diet as well as differences in daylength and weather conditions between the various studies. Table 2, which summarizes the available FMR data for nonbreeding birds weighing less than 10 g, groups species by diet and removes the effects of body size (Kleiber 1947) by dividing FMR by body mass raised to the 0.64 power (the exponent relating avian FMR to mass, Nagy 1987). These data hint that diet and/or foraging mode may affect FMR. The mass independent FMR of the four nectarivores averages 13.7 kJ/(g^{0.64}·day), and is about 50% higher than that of the two insectivorous species. Three of the nectarivores are hummingbirds, which hover while feeding, whereas one, the Eastern Spinebill (*Acanthorhynchus tenuirostris*), is an Australian honey-eater that feeds while perched. Eastern Spinebills spend about 2% of the day in flight (Paton, unpubl. data) vs. about 5% for Crowned Woodnymphs (Stiles, unpubl. data) and 20% for Anna's Hummingbirds, *Calypte anna* (Stiles 1971). The lack of an obvious correlation between time spent in flight and FMR emphasizes the importance of energy-requiring processes other than flight as determinants of FMR.

Although the granivore has the highest mass-independent FMR, it was studied in captivity during cool, windy weather—conditions which increase metabolic rate. Clearly, more data are required to confirm the hypothesized link between diet and FMR. Should such a relation be substantiated, allometric relations used to predict FMR from body size could be modified to take diet into account, thereby improving their utility.

A wide choice of allometric equations is available with which we can compare our hummingbirds' FMR. Walsberg (1983) derived an equation relating FMR to body size for birds that forage in flight. The single *Chalybura*'s FMR is 24% higher than predicted by this equation, whereas that of the nine *Thalurania* averages only 2% higher than predicted. Nagy (1987) reanalyzed the scaling of avian FMR restricting his analysis to determinations of FMR made with the DLW technique. The FMR of *Thalurania* is 26% greater than predicted by Nagy's equation for all birds and 140% greater than predicted by his nonpasserine equation. Nagy's nonpasserine equation is strongly biased in favor of large birds and does not seem to apply to hummingbirds. For example, it predicts a FMR for *C. anna* that is only 46% of the observed value (Powers, pers. comm.). Furthermore, Nagy's equations are derived mainly from data for birds during the breeding season when FMR is thought to be highest, whereas all of the hummingbirds studied thus far were nonbreeding. Thus, the FMR of tropical

hummingbirds seems representative of species which forage in flight, but much higher than predicted for nonpasserines that do not forage in flight. These data do not support the notion that tropical birds necessarily have low FMR.

The relative power requirement of different species can be compared by calculating the ratio of FMR to rest phase BMR (King 1974), with large ratios indicating "hard working" species. Data for our hummingbirds' BMR are unavailable, but using BMR values predicted from mass, we calculate FMR/BMR ratios of 6.1 and 7.0 (Table 2). These values, which would be the highest reported for any bird, suggest that hummingbirds are the hardest working of all the birds—a view consistent with their small size and intense activity. These ratios seem unrealistically high, however, as theoretical considerations and empirical measurements indicate that the maximum FMR/BMR ratio is about 5.7 (for review, see Weathers and Sullivan, in press). This suggests that our hummingbirds' actual BMR may be higher than predicted.

Surprisingly few reliable data on hummingbird BMR are available. Those that do exist indicate that at least some hummingbirds have higher BMR than predicted by the equations of Aschoff and Pohl (1970). The BMR of *Oreotrochilus estella* is 81% higher (Carpenter 1976), and that of Anna's Hummingbird is 67% higher (Powers, unpubl. data), than predicted. The FMR/BMR ratio of the temperate Anna's Hummingbird, 3.5 (Table 2), is similar to that of other nonpasserines (Weathers and Sullivan, in press). A similar 3.5 ratio for *Thalurania* would require a BMR 167% higher than predicted from the Aschoff and Pohl equation. Clearly, BMR measurements of tropical hummingbirds are needed to resolve this issue.

WATER INFLUX

Water influx equals water efflux provided body mass and water content do not change during the measurement interval, as was essentially true for our hummingbirds (Table 1). Water influx averaged 2,001 ml/(kg·day) ($n = 2$) for *Chalybura* and 2,392 ml/(kg·day) ($n = 12$) for *Thalurania*. These values, respectively 267% and 286% of what would be predicted from the birds' mass (Nagy and Peterson 1988), are the highest relative water influx rates reported for any bird species (for review, see Nagy and Peterson 1988). Indeed, *Thalurania* males turn over an equivalent of 366% of their total body water content each

day, a rate exceeding that of some amphibians (Nagy and Peterson 1988).

High water flux rates in our tropical hummingbirds probably result from three factors: a mesic environment, their high FMR, and a liquid diet. Although the relative importance of these three factors is difficult to discern, data for temperate nectarivores suggest a substantial environmental contribution. Daily water influx of Anna's Hummingbird (1,640 ml/kg·day) and the Eastern Spinebill (905 ml/kg·day) is considerably lower than that of the tropical hummingbirds, whereas their field metabolic rates are fairly similar (Table 2).

Comparable water flux data for other very small birds suggest that diet may surpass body size as a determinant of flux rate (Table 3). Nagy and Peterson (1988) proposed using the ratio of daily water flux rate (ml/day) to daily field metabolic rate (kJ/day)—the so-called "water economy index"—to compare directly water use of different species independent of body size or taxa effects. For very small birds, the water economy index seems to reflect the water content of the diet, being highest in nectarivores, intermediate in insectivores, and lowest in the granivore. However, no such correlation is apparent for vertebrates in general (Nagy and Peterson 1988), suggesting that differences across taxonomic groups may obscure such patterns.

For *Thalurania* males recaptured within 1 day of release, we can partition water influx into that due to metabolic water formation, diet, and drinking plus vapor input. Metabolic water input, calculated assuming 0.662 μ l of water were formed for each milliliter of CO₂ produced (Schmidt-Nielsen 1964; for a diet of 10% insects and 90% nectar), averaged 1.17 ml/day, or 10% of the total input (Table 1). Dietary water input was calculated from the birds' FMR assuming that the birds obtained 4.46 kJ of energy for each milliliter of dietary water ingested. This value was estimated as follows: the average sugar concentration of *H. imbricata* nectar is 0.65 M (Stiles 1975), which is equivalent to 3.76 kJ/ml of nectar. Each milliliter of nectar contains 0.886 ml of water, which gives an effective energy value of 4.14 kJ/ml of water obtained from nectar (3.76 kJ/ml nectar divided by 0.886 ml water/ml nectar). Assuming that the insects which our hummingbirds ate were 67% water and had a metabolizable energy content of 4.94 kJ/g wet weight (Ricklefs 1974), the birds would obtain 7.37 kJ/ml water from insects. Assuming a diet of 90%

TABLE 3. Water influx of very small birds.

	Mass, g	n	Water influx		Water economy index, ml/kJ	Source
			ml/day	% Pred*		
Nectarivores						
<i>Calypte anna</i>	4.5	8	7.38	190	0.23	Powers and Nagy 1988
<i>Thalurania colombica</i>	4.9	12	11.81	286	0.31	This study
<i>Chalybura urochrysa</i>	7.2	2	14.38	267	0.24	This study
<i>Acanthorhynchus tenuirostris</i>	9.7	6	8.78	132	0.17	Weathers and Paton, unpubl. data
Frugivore						
<i>Zosterops lateralis</i>	9.5	9	10.78	164	0.25	Rooke et al., unpubl. data
Insectivores						
<i>Auriparus flaviceps</i>	6.6	11	3.13	62	0.10	Webster and Weathers, unpubl. data
<i>Malurus cyaneus</i>	8.2	2	5.36	91	0.16	Weathers and Paton, unpubl. data
Granivore						
<i>Estrilda troglodytes</i>	6.7	9	1.49	46	0.03	Weathers and Nagy 1984

* Predicted from mass by equations of Nagy and Peterson (1988) for birds in the field or in captivity, as appropriate.

nectar and 10% insects, the hummingbirds would obtain 4.46 kJ/ml dietary water ($[0.9 \times 4.14] + [0.1 \times 7.37]$). Dividing FMR by this factor gives an average dietary water input of 8.5 ml/day, or 73% of the total water input (Table 1).

Subtracting metabolic water and dietary water input from total water influx gives the water input due to drinking and/or vapor input across respiratory surfaces. Our calculations suggest that *Thalurania* males gained an average of 1.95 ml of water per day (17% of the total input) via these pathways (Table 1). This value seems unreasonably high, however, and lower values would result from changing the assumptions upon which it is based. For example, if our hummingbirds gained all of their energy from nectar (i.e., they did not eat insects), the input due to "drinking" would be only 0.22 ml/day. Drinking would also be less if the floral nectar were more dilute than 0.65 M. However, it is unlikely that rain diluted the floral nectar, thereby increasing the dietary water input, since nectar of *H. imbricata* is well protected in a deep nectar chamber. Moreover, data on nectar concentration on rainy vs. sunny days indicate no differences (Stiles, unpubl. data).

Because of their liquid diet and humid environment, our hummingbirds probably did not drink much water. However, we have observed these birds drinking from dripping foliage occasionally after rains or early in the morning. Also, the birds bathe in wet moss on branches or leaves. Following such bathing or after periods of heavy rain, they usually preen vigorously and

preening as a percentage of time spent perching is higher on rainy than on sunny days (25% vs. 7%; Stiles, unpubl. data). Ingestion of water incidental to preening wet plumage is suggested by the data for birds no. 13, 17, 24, and 26 which experienced heavy rain during several hours of their measurement interval (no rain fell during the time the other individuals were being measured). The average water input due to drinking and/or vapor for these four individuals is higher than that of the other birds (3.1 ml/day vs. 1.0 ml/day; Table 1), although the difference is not statistically significant (Mann-Whitney *U*-test). Interestingly, the mean rate of CO₂ production was identical during rainy and dry measurement periods, suggesting that these tropical birds may not incur additional energy costs during periods of rain. Presumably any increment in thermoregulatory costs during rainy periods (e.g., Lustick and Adams 1977) was offset by a reduction in activity. Aggressive behavior, insect catching, and miscellaneous flying are reduced in light rain and virtually eliminated in heavy rain, although at least territorial males continue to feed in all but the heaviest downpours (Stiles, pers. observ.).

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LITERATURE CITED

- ASCHOFF, J., AND H. POHL. 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergrösse. *J. Ornithol.* 111:38-47.
- CARPENTER, T. M. 1948. Tables, factors, and formulas for computing respiratory exchange and biological transformations of energy. 4th ed. Carnegie Inst. Publ. 303C. Washington, DC.
- CARPENTER, F. L. 1976. Ecology and evolution of an Andean hummingbird (*Oreotrochilus estella*). *Univ. Calif. Publ. Zool.* 106:1-74.
- CRUMB, B. G., J. B. WILLIAMS, AND K. A. NAGY. 1985. Can tritiated water-dilution space accurately predict total body water in chukar partridges? *J. Appl. Physiol.* 59:1383-1388.
- KING, J. R. 1974. Seasonal allocation of time and energy resources in birds. *Publ. Nuttall Ornithol. Club* 15:4-70.
- KLEIBER, M. 1947. Body size and metabolic rate. *Physiol. Rev.* 27:511-541.
- LUSTICK, S., AND J. ADAMS. 1977. Seasonal variation in the effects of wetting on the energetics and survival of Starlings (*Sturnus vulgaris*). *Comp. Biochem. Physiol.* 56A:173-177.
- NAGY, K. A. 1980. CO₂ production in animals: analysis of potential errors in the doubly labeled water method. *Am. J. Physiol.* 238:R466-R473.
- NAGY, K. A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monogr.* 57:111-128.
- NAGY, K. A., AND D. P. COSTA. 1980. Water flux in animals: analysis of potential errors in the tritiated water method. *Am. J. Physiol.* 238:R454-R465.
- NAGY, K. A., AND C. C. PETERSON. 1988. Scaling of water flux rate in animals. *Univ. Calif. Publ. Zool.* 120:1-172.
- NAGY, K. A., R. B. HUEY, AND A. F. BENNETT. 1984. Field energetics and foraging mode of Kalahari lacertid lizards. *Ecology* 65:588-596.
- OBST, B. S., K. A. NAGY, AND R. E. RICKLEFS. 1987. Energy utilization by Wilson's storm-petrel (*Oceanites oceanicus*). *Physiol. Zool.* 60:200-210.
- POWERS, D. R., AND K. A. NAGY. 1988. Field metabolic rate and food consumption by free-living Anna's Hummingbirds (*Calypte anna*). *Physiol. Zool.* 66:500-506.
- RICKLEFS, R. E. 1974. Energetics of reproduction in birds. *Publ. Nuttall Ornithol. Club* 15:152-292.
- RICKLEFS, R. E., AND J. B. WILLIAMS. 1984. Daily energy expenditure and water-turnover rate of adult European Starlings (*Sturnus vulgaris*) during the nesting cycle. *Auk* 101:707-716.
- RICKLEFS, R. E., D. D. ROBY, AND J. B. WILLIAMS. 1986. Daily energy expenditure by adult Leach's storm-petrels during the nesting cycle. *Physiol. Zool.* 59:649-660.
- SCHMIDT-NIELSEN, K. 1964. Desert animals. Oxford Univ. Press, New York.
- STILES, F. G. 1971. Time, energy, and territoriality of the Anna hummingbird (*Calypte anna*). *Science* 173:818-820.
- STILES, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* 56:285-301.
- STILES, F. G. 1980. The annual cycle in a tropical wet forest hummingbird community. *Ibis* 122:322-342.
- STILES, F. G., AND L. L. WOLF. 1973. Techniques for color-marking hummingbirds. *Condor* 75:244-245.
- WALSBERG, G. E. 1983. Avian ecological energetics, p. 161-220. *In* D. S. Farner, J. R. King, and K. C. Parkes, [eds.], *Avian biology*. Vol. 7. Academic Press, New York.
- WEATHERS, W. W. 1977. Temperature regulation in the dusky munia, *Lonchura fuscans* (Cassin) (Estrildidae). *Aust. J. Zool.* 25:193-199.
- WEATHERS, W. W. 1979. Climatic adaptation in avian standard metabolic rate. *Oecologia (Berl.)* 42: 81-89.
- WEATHERS, W. W. 1986. Thermal significance of courtship display in the blue-black grassquit (*Volinia jacarina*). *Natl. Geogr. Res.* 2:291-301.
- WEATHERS, W. W., AND K. A. NAGY. 1984. Daily energy expenditure and water flux in black-rumped waxbills (*Estrilda troglodytes*). *Comp. Biochem. Physiol.* 77A:453-458.
- WEATHERS, W. W., AND K. A. SULLIVAN. In press. Juvenile foraging proficiency, parental effort, and avian reproductive success. *Ecol. Monogr.*
- WEBSTER, M. D., AND W. W. WEATHERS. 1989. Validation of the single-sample doubly labeled water method. *Am. J. Physiol.* 256 (Regulatory Integrative Comp. Physiol. 25):R572-R576.
- WILLIAMS, J. B., AND K. A. NAGY. 1985. Water flux and energetics of nestling savannah sparrows in the field. *Physiol. Zool.* 58:515-525.
- WOOD, R. A., K. A. NAGY, S. MACDONALD, S. T. WAKAKUWA, R. J. BECKMAN, AND H. KAAZ. 1975. Determination of oxygen-18 in water contained in biological samples by charged particle activation. *Anal. Chem.* 47:646-650.