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# FIELD METABOLIC RATE AND FOOD CONSUMPTION BY FREE-LIVING ANNA'S HUMMINGBIRDS (*CALYPTE ANNA*)<sup>1</sup>

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We measured CO<sub>2</sub> production and water flux using doubly labeled water in wild Anna's hummingbirds living in the Santa Ana Mountains of Southern California during autumn (September) of 1981. The estimated field metabolic rate (FMR) of a hummingbird maintaining a constant body mass (mean 4.48 g) is about 32 kJ/day, which is 5.2 times basal metabolic rate (BMR). Metabolic rates during daylight hours were about 6.8 × BMR, less than one-half that expected for an Anna's hummingbird in continuous hovering flight. We estimated nighttime metabolism to be near 2.1 × BMR, which is about what would be expected for a normothermic, resting bird experiencing cool air temperatures (as low as 15 C) but much higher than expected if torpor were employed. Water influx was about 164% of body mass per day in birds maintaining a constant mass. Most of this water intake was in the form of sucrose solution from feeders in the area, but some probably came from insects eaten by the birds. Hummingbirds probably did not drink liquid water from streams or ponds during the measurement period.

## INTRODUCTION

Walsberg (1983) suggested that small birds (<10 g) are more intensely active than larger birds and therefore should have a high mass-specific field metabolic rate (FMR) on a daily (24 h) basis. Among small birds, hummingbirds are very active, allocating 12%–25% of their diurnal time budget to flight (see Calder 1974 for review). This results from the frequent performance of territorial behaviors involving flight (chases and displays) and from the hummingbird's feeding technique. Because of their small size and extensive time commitment to flight, hummingbirds should have among the highest mass-specific FMRs of any bird. Direct measurements of FMR on hummingbirds are lacking, however.

Attempts to estimate hummingbird

FMR indirectly through time-budget analysis (e.g., Pearson 1950, 1954) suffer from two problems: (1) inaccurate characterization of the thermal environment can cause large errors in estimates of FMR (Weathers et al. 1984; Williams and Nagy 1984a), and (2) it is difficult to determine to what extent torpor is utilized at night. Therefore, it is preferable to use a method that makes direct measurements of FMR on free-living hummingbirds.

We measured FMR in free-living Anna's hummingbirds (*Calypte anna*) using the doubly labeled water (DLW) method (Nagy 1980, 1983; Nagy and Costa 1980). The DLW technique also provides measurements of water flux. These are of interest because many species of hummingbirds appear, at least under moderate conditions, to consume excessive amounts of water (Calder 1979; Calder and Hiebert 1983) with their diet, which consists primarily of dilute floral nectar (typically 20% sugar; Baker 1975). Our goals in this study were: (1) to examine how hummingbirds, among the smallest of homeotherms, use energy in their natural environment, and (2) to contribute to allometric models used to predict physiological parameters based on body mass (reviewed by Calder 1984; Schmidt-Nielsen 1984; Nagy 1987; Nagy and Peterson 1988).

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## MATERIAL AND METHODS

### STUDY SITE AND ANIMALS

*Calypte anna* is a small hummingbird (4.5 g) that inhabits the chaparral areas of California and the deserts of Arizona and Mexico. We chose *C. anna* for this study because this species is abundant and because much information on their physiology and ecology is already available (Pearson 1950, 1954; Bartholomew, Howell, and Cade 1957; Stiles 1971; Bartholomew and Lighton 1986; Powers 1987).

We studied Anna's hummingbirds at the Tucker Wildlife Sanctuary in the Santa Ana Mountains, Orange County, California, during September 1981, prior to the beginning of the breeding season. The weather was fair during the study, with minimum air temperatures averaging 15.5 C and maximum temperatures averaging 33 C in the shade. The photoperiod was almost exactly 12L:12D.

The sanctuary staff supported hummingbirds by maintaining feeders with 20% sucrose solution ad lib. year-round. The dependence of birds on feeders should not seriously affect our measurements of FMR or water flux because: (1) time budgets for our birds (Powers 1987) were similar to those for wild birds feeding on flowers (Stiles 1971), suggesting that feeders did not affect the daily amount of activity, and (2) the mean sugar content of feeder solution is similar to that of floral nectar.

Twenty-nine hummingbirds were captured in mist nets, weighed to the nearest 10 mg on a Mettler P1200 top-loading balance, given a unique mark on the breast feathers with model airplane paint, and given an injection in the thigh muscles of 0.0505 ml of water containing 55.6  $\mu$ Ci of tritium and 95 atoms percent oxygen-18. After holding the birds for 1 h to allow injected isotopes to equilibrate with body fluids (Williams and Nagy 1984b), we took a blood sample (10–20  $\mu$ l) from a femoral vein or artery and released the birds where they were captured. Twenty microliters is approximately 7% of the total blood volume of a 4.5-g bird, which should not seriously affect an active species like *C. anna* (see Kovach, Szasz, and Pilmayer 1969). Injected birds were recaptured opportunistically

during the 2 days following injection. Each of the eight birds we recaptured was weighed, and a blood sample was taken before they were released again. One additional bird was sampled but not injected in order to measure background levels of isotopes in the blood.

### ISOTOPE ANALYSES

Blood samples were flame-sealed in heparinized glass capillary tubes and placed on ice in the field pending transport to the University of California, Los Angeles. There, the samples were microdistilled under vacuum to yield pure water, which was then analyzed for tritium by liquid scintillation counting, and for oxygen-18 by proton activation analysis (Wood et al. 1975; Nagy 1983). Rates of CO<sub>2</sub> production and water flux were calculated using the equations for linearly changing body water volumes (Nagy 1980; Nagy and Costa 1980). Energy equivalents of CO<sub>2</sub> volumes were calculated assuming that a pure sugar (carbohydrate) diet yields 20.8 J/ml CO<sub>2</sub> (Nagy 1983). Body water volumes, required in the CO<sub>2</sub> and water flux calculations, were estimated from oxygen-18 dilution spaces (Nagy 1975, 1980) for initial capture times. We estimated body water volume at recapture as the product of fractional water content at initial capture and final body mass (assuming fractional water content did not change). This assumption may introduce errors of several percent into calculated FMR and water flux values (Nagy 1980; Nagy and Costa 1980), depending on actual changes in body composition as body mass increased or decreased.

### STATISTICS

Results are given as means  $\pm$  1 SD. Linear regression analyses were done using the method of least squares (Zar 1974). Regressions were considered statistically significant if  $P \leq .05$  via an *F*-test.

### RESULTS AND DISCUSSION

Mean body mass of the eight hummingbirds that we recaptured was  $4.48 \pm 0.51$  g (table 1). Body water volumes (oxygen-18 dilution spaces) at the time of injection averaged  $63.4 \pm 2.5\%$  of body mass.

Hummingbirds may be expected to gain

TABLE 1

BODY MASSES AND RATES OF CO<sub>2</sub> PRODUCTION AND WATER INFLUX IN FREE-LIVING ANNA'S HUMMINGBIRDS DURING AUTUMN IN SOUTHERN CALIFORNIA

Bird No.	Sex	Mean Mass (g)	Mass Change (%/day)	Measurement Interval (h)	Percent Darkness during Measurement <sup>a</sup>	CO <sub>2</sub> Production (ml g <sup>-1</sup> h <sup>-1</sup> )	Water Influx (ml kg <sup>-1</sup> day <sup>-1</sup> )
2 . . . . .	M	4.55	-1.2	31.4	42.6	10.9	1,330
7 . . . . .	M	4.45	+13.7	6.7	21.8	19.8	3,330
8 . . . . .	M	4.32	-7.0	7.2	26.7	15.2	1,350
10 . . . . .	F	5.44	-17.5	43.0	56.2	10.4	326
13 . . . . .	F	3.82	-5.7	25.2	52.2	8.4	1,120
14 . . . . .	M	4.90	-26.4	23.0	47.8	8.4	712
19 . . . . .	M	3.95	-49.5	10.6	99.6	7.1	167
23 . . . . .	M	4.44	-5.6	22.1	54.6	15.7	739
Mean . . . . .		4.48	-12.4	. . .	. . .	. . .	. . .
SD . . . . .		.51	19.0	. . .	. . .	. . .	. . .

<sup>a</sup> Daylight began at 5:44 A.M. and ended at 17:40 P.M. PDT. This includes civil twilight.

body mass during daylight hours when they feed and lose body mass at night when they fast. Our measurement intervals in this study included different portions of daylight and nighttime. One bird (no. 19) that was injected at dusk and recaptured at dawn lost 22% of its body mass overnight (a rate equivalent to 49.5% of body mass over a 24-h period), and it had the lowest FMR and water influx rate measured in this study (table 1). Percent daily change in body mass was negatively correlated with percent darkness during the measurement interval ( $r^2 = 0.76$ ,  $P < .01$ ). Most of our birds lost body mass during measurement intervals, and average body mass change was negative (table 1). Thus, we did not calculate mean values for FMR and water flux in table 1 to represent the steady-state situation for Anna's hummingbirds (useful for comparative purposes), but instead we estimated these values by means of regression techniques.

In DLW studies, it is preferable to make measurements over periods having multiples of 24 h. However, this was not possible with our hummingbirds, which were recaptured after periods ranging from 7 to 43 h (table 1). Such variation can cause methodological errors of up to 15% in calculated water flux rates (Nagy and Costa 1980), because instantaneous rates of actual water flux probably changed during the measurement period, thereby violating

one of the assumptions in the labeled water method. However, this variation does not cause errors in calculated CO<sub>2</sub> production rates because both isotopes (tritium and oxygen-18) vary in parallel, and the errors cancel (Nagy 1980). Moreover, the different measurement intervals include differing amounts of daytime activity and nighttime rest, affording us the opportunity to estimate the field metabolic costs of each by regression analysis.

#### FIELD METABOLIC RATE

Hummingbird 19, which was released in the evening after dark and recaptured early the next morning, spent 99.6% of its measurement period in darkness and had the lowest field metabolic rate (table 1). Birds having the greatest portion of their measurement interval during daylight hours had the highest FMRs. The correlation between FMR and percent of time in darkness (fig. 1) is significant ( $P = .05$ ), and the regression line is described by the equation  $y = 18.6 - 0.13x$ , with  $r^2 = 0.50$ . The intercept, 18.6 ml CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>, is an estimate of the metabolic rate of an Anna's hummingbird during its daytime activity period (% night = 0). This value is about 6.8 times basal metabolic rate (BMR, 2.73 ml CO<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup>, calculated from Lasiewski's [1963] "minimum metabolism," assuming a respiratory quotient [RQ] of 0.71 for lipid metabolism). Metabolic rate dur-

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ing hovering flight is about  $41 \text{ ml CO}_2 \text{ g}^{-1} \text{ h}^{-1}$  (assuming  $\text{RQ} = 1.0$  and using values in Bartholomew and Lighton [1986]), which is some 15 times higher than BMR and is more than twice our estimates of daytime metabolic rate. Metabolic rate while perching is about  $16 \text{ ml CO}_2 \text{ g}^{-1} \text{ h}^{-1}$  (assuming  $\text{RQ} = 1.0$  and using the measurement from Pearson [1950] at 24 C), which is 15% lower than our estimates of daytime metabolic rate. These latter two comparisons support earlier behavioral observations that Anna's hummingbirds spend as much as 80% of their daytime hours perching (Pearson 1954; Stiles 1971).

Similarly, the intercept at percent night = 100,  $5.6 \text{ ml CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ , is an estimate of a bird's metabolic rate at night. This value,  $2.1 \times \text{BMR}$ , is close to that expected for a resting *Calypte anna* exposed to air temperatures that dropped to a low of 15.5 C (see dashed lines in fig. 1). Metabolic rates of torpid birds are much lower (ca.  $0.2\text{--}0.8 \text{ ml CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ ; see fig. 1), suggesting that our hummingbirds did not utilize torpor extensively on the nights we studied them.

We can estimate the FMR of an Anna's hummingbird that is maintaining a constant body mass (steady state) from a plot of metabolic rate versus rate of body mass change (fig. 2). The predicted metabolic rate when mass change rate is zero is  $14.2 \text{ ml CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ . As these birds were eating mostly a sugar solution, we converted metabolic rates from units of  $\text{CO}_2$  to heat units using the factor  $20.8 \text{ J/ml CO}_2$  (for carbohydrate), which is equivalent to  $7.1 \text{ kJ g}^{-1} \text{ day}^{-1}$ , or about  $31.8 \text{ kJ/day}$  for a 4.48-g bird. This is  $5.2 \times \text{BMR}$ , and is very similar to the predicted values of  $7.44 \text{ kJ g}^{-1} \text{ day}^{-1}$  (Calder 1974; as recalculated from Lasiewski 1963) and  $7.2 \text{ kJ g}^{-1} \text{ day}^{-1}$  (Walsberg 1983).

WATER FLUX RATE

We estimated the rate of water flux in a hummingbird maintaining a constant body mass in the field by using the same regression analysis technique used above with FMR. The regressions of water influx and efflux on the rate of body mass change are both statistically significant ( $P < .05$ ), and both intersect the weight-maintenance line at a water flux rate of about

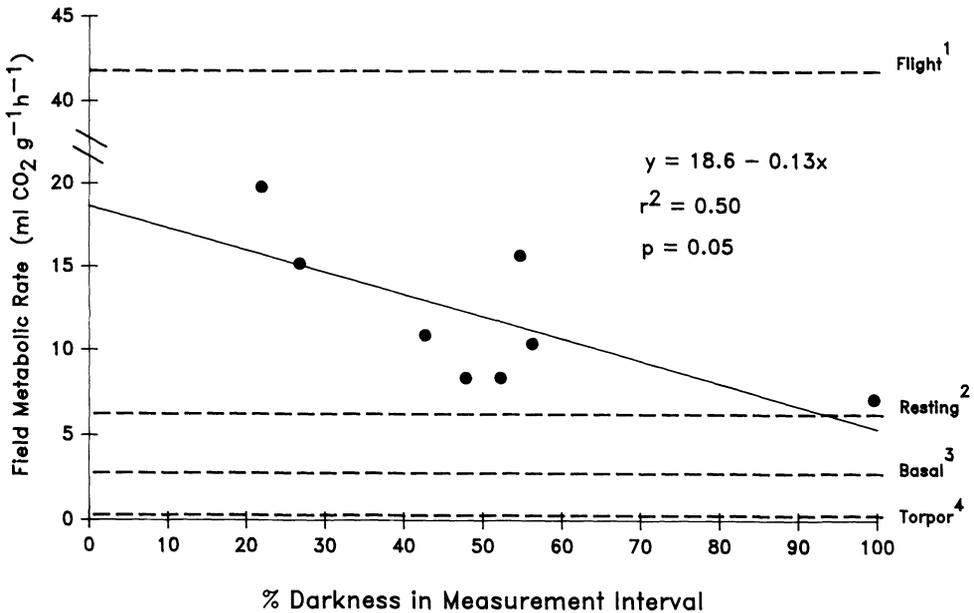


FIG. 1.—Relation of field metabolic rate of Anna's hummingbirds measured by doubly labeled water to the percent darkness of their measurement interval. The dashed lines represent  $\text{CO}_2$  production for various metabolic states derived from the following studies: <sup>1</sup>Bartholomew and Lighton (1986), <sup>2</sup>Lasiewski (1963) for birds at 15.5 C, <sup>3</sup>Lasiewski (1963), <sup>4</sup>Pearson (1950, 1954), Bartholomew et al. (1957), and Lasiewski (1963) for birds at 17 C.

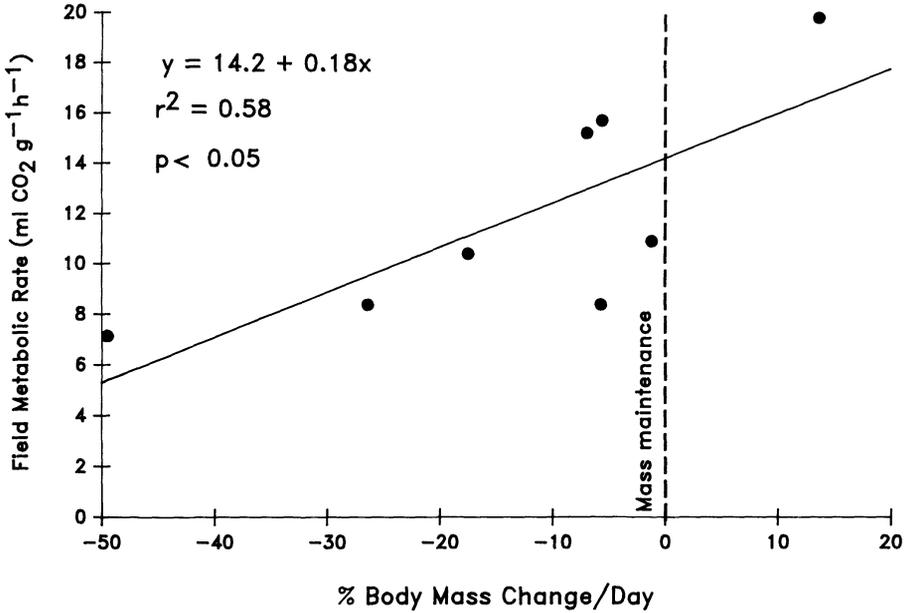


FIG. 2.—Relation of field metabolic rate of Anna’s hummingbirds measured by doubly labeled water to the percent change in body mass per day. The dashed line represents steady state.

1,640  $\text{ml kg}^{-1} \text{day}^{-1}$  (fig. 3). Thus, a 4.48-g Anna’s hummingbird was turning over about 164% of its body mass, or 7.35 ml of water each day during our study. This is

89% higher than predicted for a bird this size (Nagy and Peterson 1988) and is among the highest mass-specific water flux rates ever measured in free-ranging birds.

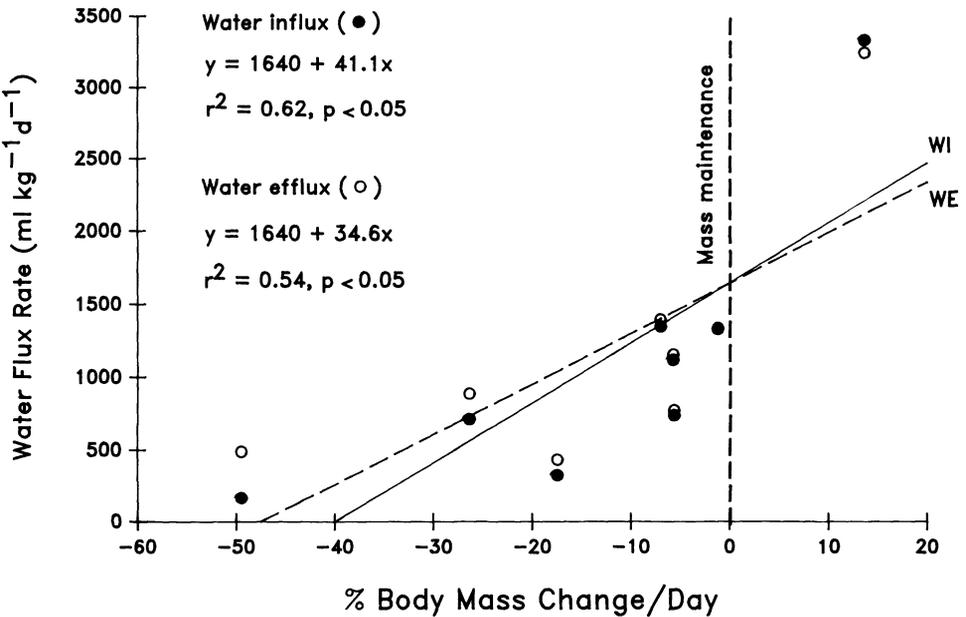


FIG. 3.—Relationship of water influx and efflux measured by doubly labeled water to the percent change in body mass per day. The solid line represents the regression of water influx (WI) and the dashed line represents the regression of water efflux (WE).

High water fluxes have also been measured in the Phainopepla, *Phainopepla nitens* (Weathers and Nagy 1980;  $945 \pm 255$  ml  $\text{kg}^{-1} \text{day}^{-1}$ ), and in Silvereyes, *Zosterops lateralis* (650–2,200 ml  $\text{kg}^{-1} \text{day}^{-1}$ ; Rooke, Bradshaw, and Langworthy 1983), both of which eat succulent fruits.

## FEEDING RATE

The rate at which an Anna's hummingbird consumes nectar can be calculated from its FMR by assuming that the bird eats just enough to satisfy its daily energy requirements (no metabolism of body fat or fat storage, as might be reflected by a constant body mass over a 24-h period). Sucrose and fructose contain about 16 kJ of total energy per gram (Weast and Selby 1967), and we assumed that all of the sugar a hummingbird consumes is assimilated (see Karasov et al. 1986). To obtain 31.8 kJ of metabolizable energy, a hummingbird must consume 1.98 g of sugar. The sugar solution and flower nectar available to our birds contained about 0.20 g sugar per gram solution (Powers 1987), so a hummingbird should consume 9.9 g of solution to meet its energy requirements.

We can compare this estimate of feeding rate with another one based on water influx rate. If hummingbirds did not drink, and ate only sugar solution, then their only sources of water (other than water vapor

diffusing across lungs and skin) would be the preformed water in the food and the water formed from the sugar upon its oxidation. One gram of sugar solution contained 0.80 g of preformed water, and the 0.20 g of sucrose should yield 0.11 g of "metabolic" water (Nagy 1983), for a total of 0.91 g of water per gram solution. Thus, a water influx rate of 7.35 ml/day is equivalent to a feeding rate of 8.08 g of solution per day, if all the assumptions above are correct. This estimate of feeding rate is 15% lower than the estimate of 9.9 g/day based on FMR (above). This discrepancy can be accounted for if hummingbirds got some of their metabolizable energy from another food source having a lower water content than did the sugar solution. Hummingbirds are known to feed on insects, presumably to obtain proteins or amino acids not readily available in nectar (Hainsworth and Wolf 1976), and insects have much lower water yields (0.06–0.08 ml  $\text{H}_2\text{O}/\text{kJ}$ ; Shoemaker and Nagy 1977) than does the sugar solution (0.27 ml/kJ). We saw some of our marked birds feeding on insects during the evening hours, so this explanation for the difference in feeding rate estimates seems likely. The observation that food consumption alone accounts for more water intake than was actually measured indicates that it is unlikely that the marked hummingbirds drank any liquid water from nearby sources.

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