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Diurnal Variation in Mass, Metabolic Rate, and Respiratory Quotient in Anna's and Costa's Hummingbirds

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Abstract

To examine how hummingbirds that do not enter torpor at night store and utilize energy, open-circuit respirometry and a strain gauge were used to measure daily variation in O_2 consumption ($\dot{V}O_2$), CO_2 production, respiratory quotient (RQ), and body mass in Anna's hummingbird, Calypte anna, *and Costa's hummingbird,* Calypte costae. *During the day, $\dot{V}O_2$ was highly variable primarily because of differences in activity among individuals. At night $\dot{V}O_2$ varied little between individuals, but mean $\dot{V}O_2$ was more than two times that predicted from body mass for resting, postabsorptive birds. For* C. anna, *mean 24-hr energy expenditure was similar to that of free-living birds. Diel mass fluctuations were large, up to 16% in both species. However, much of the observed change in mass was probably due to factors other than changes in body fat content. The RQ was well above 1.0 throughout the day, suggesting continuous deposition of fat, and RQs remained high at night (>0.85), indicating the use of carbohydrate as a metabolic substrate. Predicted crop volumes of the hummingbirds are sufficient to store the amount of feeder solution (0.25 g sucrose per mL) required to account for the observed nighttime RQs. This suggests that hummingbirds in this study were using their crop as a supplemental "energy storage depot" at night.*

Introduction

Hummingbirds are the smallest heterothermic endotherms and their mass-specific field metabolic rates (FMR) are the highest measured for any vertebrate (Powers and Nagy 1988; Weathers and Stiles 1989). For example, if hummingbirds are compared to mammals in studies where FMR was measured using doubly labeled water (see Nagy 1987 for review), the lowest mass-specific FMR measured for a hummingbird (after raising mass to the

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0.51 or 0.64 power, the respective slopes of the relationship between FMR and mass for rodents and birds, to correct for the effects of mass) is 33% higher than the highest FMR measured for a mammal (Nagy 1987; Powers and Nagy 1988). The primary reason hummingbirds have such high FMRs is because they spend large amounts of energy on maintenance (Lasiewski 1963; Kruger, Prinzinger, and Schuchmann 1982) and because their flight costs are high (Lasiewski 1963; Bartholomew and Lighton 1986). In order to satisfy their high energy demands, hummingbirds must feed frequently and thus consume large amounts of floral nectar daily if they are to maintain energy balance.

Because hummingbirds are so small and their daytime energy demands high, they are only able to store a limited amount of fat during the day. In fact, the amount of fat that can be stored by a small (3–5 g) hummingbird during the day is predicted to be only about 0.2 g (Calder 1974, eq. [46]), which would be roughly equivalent to the amount required to meet their nighttime energy needs if they remained normothermic all night at moderate temperatures. Hummingbirds that remained normothermic all night might then exhaust most of their energy reserves by the following morning (King 1972; Hainsworth 1978), leaving them vulnerable to any restrictions in energy availability that might occur.

Flowers foraged by hummingbirds are generally fragile and can be easily damaged when weather conditions are severe. For example, Gass and Lertzman (1980) determined that after a hailstorm the number of hummingbird territories that could be supported in their study area was reduced by nearly 90%. They suggested that hummingbirds were displaced because of lower food availability and were forced to either emigrate or utilize suboptimal habitat. In either case, the increased energy cost of locating food or foraging would cause a hardship for hummingbirds, especially if fat reserves are limited.

Hummingbirds can reduce the impact of low food availability, and conserve energy reserves, by entering torpor at night. During torpor, metabolic rate is reduced up to 10-fold (Pearson 1950; Lasiewski 1963; Hainsworth and Wolf 1970; Kruger et al. 1982), which would conserve almost their entire fat reserve if they remained in torpor all night. Whether hummingbirds regularly use torpor at night is uncertain (Hainsworth, Collins, and Wolf 1977; Kruger et al. 1982), however, and will require further study. Frequent use of torpor might be undesirable because it would increase the risk of predation (Hainsworth et al. 1977) and, in the case of incubating females, retard growth of developing embryos (Calder and Booser 1973). If these factors are important in determining whether torpor is used at night, then

perhaps hummingbirds remain normothermic whenever possible and conserve fat stores in some other manner.

To address questions about energy storage and the nocturnal fast, I examined daily rhythms of metabolic rate, body mass, and respiratory quotient (RQ) in Anna's hummingbird (*Calypte anna*) and Costa's hummingbird (*Calypte costae*). The RQ is the ratio of CO_2 produced to O_2 consumed during metabolism. This ratio varies for different metabolic substrates (e.g., 0.7 for fat and 1.0 for carbohydrate; Kleiber 1975) and can be used as an indicator of what substrate an animal is metabolizing. The above measurements provide information related to both storage and utilization of energy and allow me to examine the diel energy balance of hummingbirds that remain normothermic all night.

Material and Methods

Research Animals

I used mist nets to capture five male and one female *Calypte costae* at Palm Desert, Riverside County, California, in March 1984 (California Fish and Game permit no. 2170) and ten male *Calypte anna* at the Tucker Wildlife Sanctuary, Orange County, California, in October 1986 (California Fish and Game permit no. 2132). The birds were transported to the University of California, Davis, and housed individually in 1 m × 0.5 m × 0.5 m cages at a constant temperature (28° ± 1°C) and photoperiod (12L:12D) for at least 3 mo prior to measurement. I fed the birds a purified liquid diet containing 19.9% carbohydrate, 0.9% protein, 0.9% fat, and 2.1% essential vitamins, minerals, and nutrients ad lib. (Brice and Grau 1989). The energy content of the diet was 15.1 kJ dry weight. All birds maintained mass over the course of the study.

Protocol

Metabolism Measurements. I measured O_2 consumption ($\dot{V}O_2$) and CO_2 production ($\dot{V}CO_2$) with an open-circuit, positive-pressure respirometry system. Body mass was measured during the respirometry trials with a perch connected to a strain gage. All measurements were made continuously for 24 h on birds held in a metabolism chamber (described below) at a constant temperature (28°C) and photoperiod (12L:12D). Birds were placed in the metabolism chamber 2 h prior to beginning data collection. Measurements began and ended at 1100 hours. The dark phase in both the animal room and metabolism chamber was from 1900–0700 hours

for *C. anna* and from 1800–0600 hours for *C. costae*. Food (purified diet) was provided ad lib. in a 12-cm^3 syringe suspended from the top of the chamber.

I used a 31 cm × 16 cm × 21 cm Plexiglas metabolism chamber that allowed room for short flights and hover feeding. The floor of the chamber was made of aluminum to enhance thermal equilibration. Air temperature inside the chamber was monitored with a Cu-Cn thermocouple and recorded to the nearest 0.1°C with a Sensortek Bat-12. Thermocouples were calibrated against thermometers traceable to the National Bureau of Standards.

I regulated flow of dry, CO_2-free air through the metabolism chamber at 600 mL/min (STPD) by using a Brooks model 5815 mass-flow controller (previously calibrated with a bubble meter; Levy 1964) upstream from the chamber. Outlet air from the metabolism chamber passed through an infrared CO_2 analyzer (Beckman model 864 equipped with an optical filter to eliminate interference due to water vapor), then through U-tubes containing soda lime and Drierite to remove CO_2 and water vapor, and finally through an O_2 analyzer (Applied Electrochemistry model S-3A). Prior to each run I calibrated the CO_2 analyzer with certified gas standards and the O_2 analyzer with dry, CO_2-free room air, assuming an O_2 concentration of 20.95%. I measured the water content of outlet air with a General Eastern model 1100DP dew-point hygrometer (Bernstein et al. 1977). Accuracy of the hygrometer was verified gravimetrically with the methods of Bernstein et al. (1977). Data recording and analysis were done using a BBC Acorn microcomputer as described by Lighton (1985). Output from the analyzers was recorded every 12 sec and averaged each hour. I measured the fractional concentration of O_2 and CO_2 of inlet and outlet air to the nearest 0.001%. Oxygen consumption was calculated from equation (2) of Hill (1972) and CO_2 production from the equation in Weathers, Shapiro, and Astheimer (1980). To correct for damped responses caused by the washout characteristics of my system, I applied the "instantaneous" correction described by Bartholomew, Vleck, and Vleck (1981) to my $\dot{V}O_2$ and $\dot{V}CO_2$ data. Mass-specific metabolic values were calculated through hourly mass averages.

Body Mass Measurements. I measured body mass to the nearest 0.01 g with a strain gauge (Measurements Group model EA-06-125B2-350) attached to a brass beam from which a perch was suspended. The perch was constructed of light wire and was covered with shrink tubing to provide the birds with a good surface to grip. I calibrated the strain gauge with known weights. The drift characteristics of the strain gauge were tested by hanging a known

weight from the perch for 24 h. This apparatus allowed me to determine mass when the bird was on the perch. Output from the strain gauge was sampled every 6 s and averaged every minute with a Campbell Scientific CR21X data logger. If the bird did not perch continuously for the minute interval the mass measurement was discarded. A bird was considered to have perched continuously if the mass measurement was no more than 5% less than the previous five acceptable measurements.

Statistics

I used two sample Student's *t*-tests to compare independent data sets. Paired *t*-tests were used to evaluate data collected on the same individual under different conditions. A Kruskal-Wallis test was used to evaluate differences in hourly metabolic rates. Data are reported as mean ± 1 SD. Differences were considered significant if $P < 0.05$.

Results

Metabolic Rate

The $\dot{V}O_2$ among birds of both species was variable during the day but was less variable at night (fig. 1). Mean $\dot{V}O_2$ for *Calypte anna* was 19.28 ± 6.89 mL O_2 $g^{-1}h^{-1}$ during the day and 5.91 ± 0.98 mL O_2 $g^{-1}h^{-1}$ at night. Mean $\dot{V}O_2$ for *Calypte costae* was 18.53 ± 7.23 mL O_2 $g^{-1}h^{-1}$ during the day and 6.08 ± 0.50 mL O_2 $g^{-1}h^{-1}$ at night. Birds frequently flew around the chamber during the day and the total amount of flight activity appeared to vary among individuals. Birds exhibiting the most flight activity also had the highest daytime metabolic rates. Values for individual birds are presented in tables 1 and 2.

Visual observations suggested that feeding frequency was approximately four bouts/h and was constant for all birds used in the metabolic trials. A feeding bout could consist of a single trip to the feeder or several trips occurring over a short time interval. After the lights were turned off (dark phase), $\dot{V}O_2$ of both species stabilized at nighttime levels within 1 h (fig. 1). Mean 24-h $\dot{V}O_2$ (calculated from data in tables 1 and 2) was 12.59 ± 3.79 mL O_2 $g^{-1}h^{-1}$ for *C. anna* and 12.30 ± 3.54 mL O_2 $g^{-1}h^{-1}$ for *C. costae*.

Body Mass

Final mass was on average 1.44% ± 2.67% higher than initial mass for *C. anna* and 1.93% ± 5.02% lower than initial mass for *C. costae* at the end of

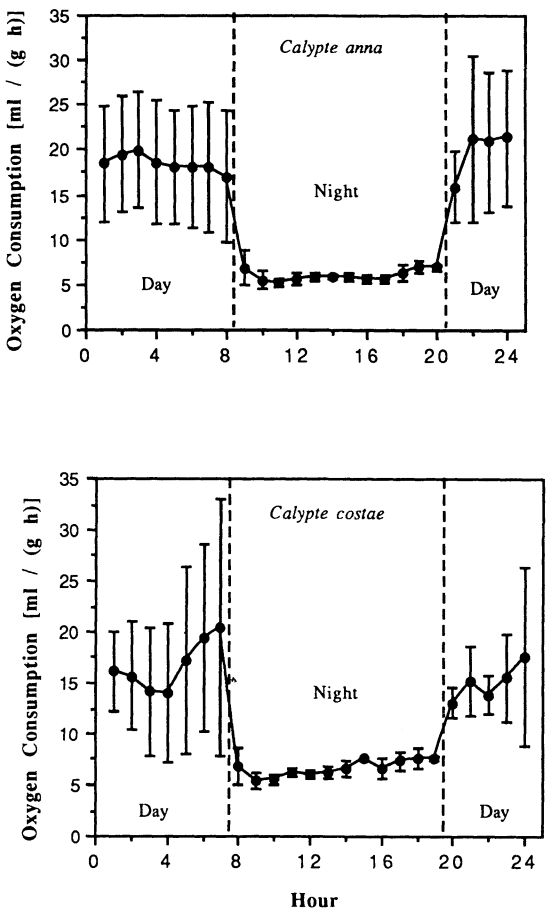

Fig. 1. Oxygen consumption for each hour of the experiment. Day (light) and night (dark) periods are separated by dashed lines. Data are 1-h averages for all birds. Vertical bars represent ± 1 SD of the mean.

each 24-h experiment (tables 1, 2). These values are not significantly different from each other and are indistinguishable from a 0% change in body mass. Body mass decreased linearly during the night in both species (fig. 2). On the basis of mean hourly mass, the rate of mass loss averaged 0.053 g h^{-1} for *C. anna* and 0.042 g h^{-1} for *C. costae.* Mean minimum mass (mass at the end of the dark phase) for *C. anna* was 4.29 ± 0.43 g and mean maximum mass (beginning of the dark phase) was 4.98 ± 0.43 g. Minimum and maximum masses for *C. anna* are significantly different (t = 21.21, df = 8) and represent an average change of 16.17% ± 3.87% over 12 h (table 1). Similarly, mean minimum mass for *C. costae* was 3.59 ± 0.36 g and mean maximum mass 4.12 ± 0.35 g. Minimum and maximum masses for *C. costae* are sig-

TABLE 1

Summary of metabolic rate, respiratory quotient (RQ), and mass data for individual Calypte anna

Bird Number	Metabolic Rate ($mL\ O_2\ g^{-1}\ h^{-1}$)[a]		RQ ($\dot{V}CO_2/\dot{V}O_2$)		24-h Mass (g)			Nighttime Mass (g)		
	Day	Night	Day	Night	Initial	Final	% Difference[b]	Initial	Final	% Difference[b]
1	14.71 ± 2.61	4.83 ± .84	1.11 ± .08	.85 ± .13	3.89	3.85	−1.04	4.42	3.55	−24.51
2	12.94 ± 1.30	5.67 ± 1.08	1.18 ± .08	.77 ± .05	4.37	4.42	1.13	4.76	4.11	−15.82
3	11.81 ± 2.77	5.41 ± .58	1.22 ± .12	.97 ± .09	4.95	4.84	−2.27	5.45	4.76	−14.50
4	13.74 ± 1.57	6.01 ± 1.06	1.16 ± .07	.77 ± .07	4.67	4.57	−2.19	5.21	4.39	−18.68
5	29.54 ± 5.93	6.88 ± .82	1.04 ± .08	.95 ± .04	4.33	4.35	.46	4.42	3.85	−14.81
6	23.18 ± 2.82	6.85 ± .82	1.09 ± .06	.91 ± .06	5.06	5.25	3.62	5.29	4.78	−10.67
7	15.51 ± 2.19	4.74 ± .75	1.21 ± .05	.89 ± .10	5.24	5.33	1.69	5.59	4.78	−16.95
8	28.07 ± 3.77	7.77 ± .66	1.07 ± .05	.93 ± .04	4.57	4.79	4.59	4.85	4.17	−16.31
9	26.98 ± 3.35	5.31 ± .29	1.10 ± .07	.91 ± .05	4.89	5.10	4 29	. . .	. . .	. . .
10	16.29 ± 4.25	5.58 ± .34	1.15 ± .09	.87 ± .06	4.68	4.88	4.10	4.79	4.23	−13.24

[a] Calculated using average mass for each hour of measurement.
[b] Calculated as 100 (Final − Initial/Final).

TABLE 2

Summary of metabolic rate, respiratory quotient (RQ), and mass data for individual Calypte costae

Bird Number	Metabolic Rate ($mL\ O_2\ g^{-1}\ h^{-1}$)[a]		RQ ($\dot{V}CO_2/\dot{V}O_2$)		24-h Mass (g)			Nighttime Mass (g)		
	Day	Night	Day	Night	Initial	Final	% Difference[b]	Initial	Final	% Difference[b]
1	13.28 ± 4.52	6.70 ± 1.40	1.25 ± .14	.84 ± .03	3.66	3.45	−6.25	3.96	3.28	−20.73
2	10.94 ± 2.18	6.22 ± .89	1.09 ± .11	.81 ± .13	4.43	4.37	−1.35	4.73	4.18	−13.16
3	27.96 ± 7.58	6.32 ± 1.02	.89 ± .10	.79 ± .03	4.35	4.23	−2.76	4.24	3.80	−11.58
4	15.86 ± 2.86	5.45 ± .75	1.17 ± .12	.84 ± .09	3.53	3.36	−5.06	3.72	3.22	−15.53
5	16.03 ± 3.38	6.26 ± .65	1.17 ± .14	.88 ± .04	3.76	3.62	−3.87	4.15	3.55	−16.90
6	27.12 ± 9.03	5.50 ± 1.42	1.08 ± .16	.91 ± .10	3.38	3.64	7.69	3.89	3.49	−11.46

[a] Calculated using average mass for each hour of measurement.
[b] Calculated as 100 (Final − Initial/Final).

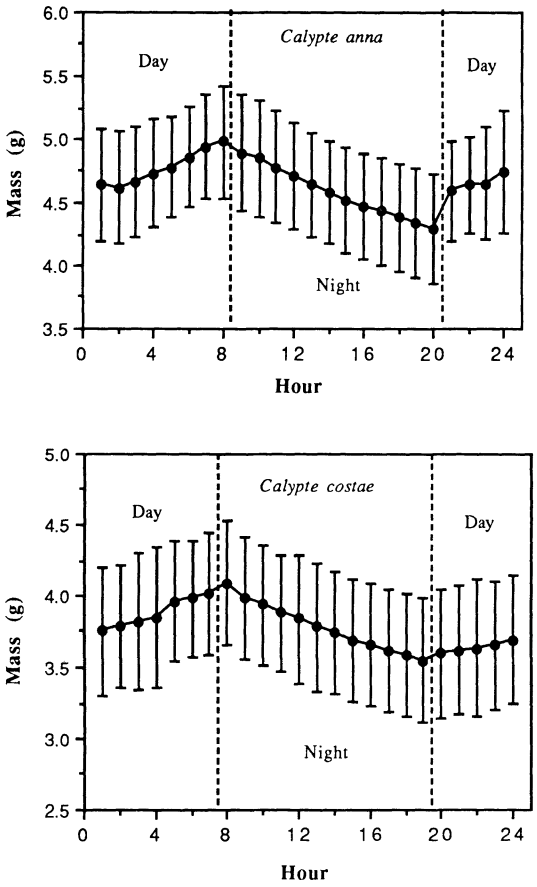

Fig. 2. Body mass for each hour of the experiment. Symbols as in fig. 1.

nificantly different as well (t = 10.15, df = 5) and represent an average change of 14.9% ± 3.58% over 12 h (table 2).

Respiratory Quotient

The RQ exceeded 1.0 during the day in both species (t = 6.97, df = 9 for *C. anna*; t = 2.15, df = 5 for *C. costae*), averaging 1.14 ± 0.06 for *C. anna* (table 1; fig. 3) and 1.11 ± 0.12 for *C. costae* (table 2; fig. 3), suggesting fat deposition. Mean nighttime RQ was 0.88 ± 0.07 for *C. anna* and 0.85 ± 0.04 for *C. costae* and was significantly lower than daytime RQ for both species (t = 7.17, df = 8, for *C. anna*; t = 5.78, df = 5 for *C. costae*). Mean 24-h RQ was 1.01 ± 0.04 for *C. anna* and 0.97 ± 0.07 for *C. costae*. Neither value is significantly different from 0.97, the RQ expected on the basis of proportion of fat, protein, and carbohydrate in the purified diet, assuming the mass and

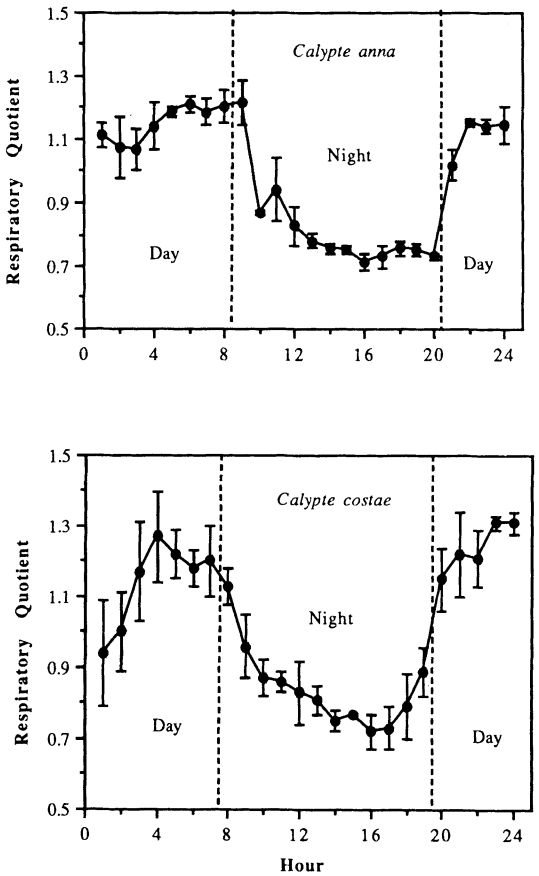

Fig. 3. Respiratory quotient for each hour of the experiment. Symbols as in fig. 1.

body composition of the birds is the same at the beginning and end of the measurement period.

Discussion

Energy Expenditure

Hummingbirds often have metabolic rates higher than that predicted on the basis of body mass (e.g., Carpenter 1976; Powers 1989; table 3). Nighttime $\dot{V}O_2$ in this study was similar to previous measurements of *Calypte anna* and *Calypte costae* that were postabsorptive and resting in the dark at 28°C (Lasiewski 1963) but were more than two times that predicted from body mass (Aschoff and Pohl 1970; table 3). Nighttime $\dot{V}O_2$ in both species probably stabilized at high levels because the T_a used in this study (28°C) was

TABLE 3

Comparison of the metabolic rate of Calypte anna *and* Calypte costae *with literature values*

	Multiple of Metabolic Measurement[a]						
	Calypte anna			*Calypte costea*			
Metabolic Measurement	Night	Day	24 h	Night	Day	24 h	Source
Minimum metabolism . .	1.5	5.0	3.3	1.9	6.0	4.0	Lasiewski (1963)
Basal MR[b]	2.3[c]	1.0[d]	4.8[c]	2.2[c]	1.1[d]	4.3[c]	Aschoff and Pohl (1970)
Nighttime resting MR . . .	.8	2.6	1.7	. . .	. . .	. . .	Powers and Nagy (1988)
Daytime resting MR	1.1	3.6	2.3	1.6	5.1	3.4	D. Powers, unpublished data
Existence MR[e]	.8	2.6	1.7	.7	2.3	1.5	Kendeigh et al. (1977)
Daytime field MR	.4	1.2	.8	. . .	. . .	. . .	Powers and Nagy (1988)
24-h field MR	.4	1.4	.9	. . .	. . .	. . .	Powers and Nagy (1988)

Note. MR = metabolic rate.

[a] Calculated as MR from present study divided by MR measurements/predictions from other studies.

[b] Compared with the allometric equations for all nonpasserine birds.

[c] Predicted using the equation for ρ phase. On the basis of mean nighttime RQ, I assumed 1 L O_2 equaled 20.44 kJ for *C. anna* and 20.37 kJ for *C. costae* (Gessaman and Nagy 1988).

[d] Predicted using the equation for α phase. On the basis of mean RQ, I assumed 1 L of O_2 equaled 20.9 kJ. I assumed the energy value of O_2 for RQs above 1.0 did not differ significantly from the energy value of O_2 when RQ = 1.0.

[e] Predicted using the equation for nonbreeding birds during the winter at 30°C. Existence metabolism was adjusted for birds at 28°C with the equations of Aschoff (1981) for thermal conductance.

slightly below their lower critical temperature (30°–33°C; Lasiewski 1963; Powers 1989). If, as an approximation, I correct nighttime $\dot{V}O_2$ on the basis of thermal conductance (approximately 0.3 mL O_2 $g^{-1}h^{-1}°C^{-1}$ for both species from the ρ-phase equation for nonpasserine birds of Aschoff [1981]) to that expected at the lower critical temperature, nighttime metabolic rate for *C. anna* and *C. costae* is still 1.6 and 2.0 times higher, respectively, than that predicted from body mass (Aschoff and Pohl 1970).

Mean 24-h metabolic rates for *C. anna* and *C. costae* (table 3) were 1.7 and 1.5 times higher, respectively, than predicted existence metabolism (metabolizable energy of caged birds provided with food and water ad lib.; Kendeigh, Dol'nik, and Gavrilov 1977, eq. [5.25]). Because the hummingbirds in my study frequently made short flights around the metabolism chamber, the high 24-h metabolic rate was probably due to the cost of flight, which is greater than that of any other vertebrate (when hovering hummingbirds consume in excess of 40 mL O_2 $g^{-1}h^{-1}$; e.g., Lasiewski 1963; Bartholomew and Lighton 1986). This high flight $\dot{V}O_2$ can contribute significantly to daytime energy expenditure (see below).

Mean daytime $\dot{V}O_2$ varied two- to threefold among individuals (tables 1, 2), probably because of differences in the amount of time that birds spent flying. Lasiewski (1963) observed similar variability in daytime $\dot{V}O_2$ of *C. costae*. He also observed that $\dot{V}O_2$ increased prior to the beginning of the nighttime portion of the daily cycle. He suggested that this increase in $\dot{V}O_2$ might be due to an increase in feeding activity. In this study, feeding rate remained constant throughout the day and mean $\dot{V}O_2$ did not increase significantly prior to the dark phase in either species (fig. 1).

The behavior of hummingbirds during metabolic measurements differed from that of wild birds in that they could not engage in the complex social interactions and foraging patterns exhibited by free-living hummingbirds (Stiles 1971, 1982; Kodric-Brown and Brown 1978; Wheeler 1980; Powers 1987). Nevertheless, daytime, nighttime, and 24-h energy expenditure, at least for *C. anna* (table 1), was similar to that of their free-living counterparts (Powers and Nagy 1988; table 3). This suggests that the time spent flying by my captive birds was similar to that of birds in the wild. Free-living hummingbirds devote on average 15%–20% of the daytime to flight (see, e.g., Pearson 1954; Stiles 1971; Ewald and Bransfield 1987), which for *C. anna* accounts for about 40% of their daytime energy cost (assuming flight $\dot{V}O_2$ = 41 mL O_2 $g^{-1}h^{-1}$; Bartholomew and Lighton 1986).

The $\dot{V}O_2$ decreased to a stable level in both species within the first hour of the night phase (fig. 1). This pattern is similar to that reported by Pearson (1954), Lasiewski (1963), and Kruger et al. (1982) for nontorpid hummingbirds at air temperatures above 12°C. On the basis of these data, hum-

mingbirds appear to achieve a stable nighttime $\dot{V}O_2$ much more quickly than other birds for which similar data are reported in the literature. Bramblings, *Fringilla montifringilla* (20 g; Aschoff and Pohl 1970), European kestrels, *Falco tinnunculus* (180 g; Masman 1986), three species of owls (*Aegolius acadicus,* 85 g; *Asio otus,* 252 g; *Asio flammeus,* 406 g; Graber 1962), and domestic fowl (1,500–3,500 g; Barott et al. 1938) do not reach a stable nighttime $\dot{V}O_2$ under laboratory conditions; rather, $\dot{V}O_2$ continues to drift downward. The European goldfinch, *Carduelis carduelis* (16 g; Gluck 1985), exhibits a pattern similar to that of the hummingbirds. One possible explanation for these data is that larger species take more time to reach a "postabsorptive" state because of lower mass-specific metabolic rates and the increased effect of specific dynamic action (SDA) that accompanies diets high in protein and fat. The domestic fowl, for example, requires up to 2 d to become "postabsorptive," during which resting metabolic rate is increased up to 18% by SDA (Barott et al. 1938). The SDA can increase resting metabolic rate as much as 45% in birds with diets high in protein (Ricklefs 1974). This should not be a major factor for hummingbirds, however, because uptake of sugar in the gut occurs quickly (Karasov et al. 1986), and the increase in metabolic rate due to SDA is only about 6% for a predominantly sucrose diet (Ricklefs 1974).

Although I did not measure body temperature, birds apparently did not enter torpor during metabolic measurements at night because their metabolic rates remained high and body mass declined (tables 1, 2; figs. 1, 2). Mean nighttime $\dot{V}O_2$ of the respective species was 3.5–10.9 times the $\dot{V}O_2$ measured in torpid *C. anna* (Pearson 1950, 1954; Bartholomew, Howell, and Cade 1957; Lasiewski 1963) and 15.8 times the $\dot{V}O_2$ measured in torpid *C. costae* (Lasiewski 1963). In addition, torpid hummingbirds have a characteristic appearance (see Carpenter and Hixon 1988 for description) that I never observed in birds during metabolic measurements or at night in their cages. Beuchat, Chaplin, and Morton (1979) also observed that *C. anna* remained normothermic at night except under extreme conditions.

Energy Storage

The amplitudes of the daily mass cycles of *C. anna* and *C. costae* are impressive when compared with other birds. Most birds lose less than 10% of their mass overnight (see, e.g., Baldwin and Kendeigh 1938; Chaplin 1974; Ketterson and Nolan 1978; Lehikoinen 1987), which is substantially less than the 15%–16% observed for hummingbirds in this study during metabolic trials. Most of the birds for which overnight mass-loss data are available are much larger (>20 g) than the hummingbirds that I studied and/or have

lower mass-specific metabolic rates than hummingbirds. Larger size and a lower metabolic rate both contribute to greater stability in body fat content. Nocturnal mass loss by small free-living hummingbirds (ca. 12%–14%; D. Powers, unpublished data) is comparable to that of hummingbirds during metabolic measurements in this study.

Although diel mass cycles reflect energy storage and utilization, they must be interpreted with caution (King 1972). Direct measurements of fat storage in hummingbirds have only been made on ruby-throated hummingbirds (*Archilochus colubris,* ca. 3.5 g) because of interest in their apparent ability to migrate across the Gulf of Mexico. Premigratory *A. colubris* contain as much as 1.7–2.6 g of fat, an amount representing nearly half their total body weight (Norris, Connell, and Johnston 1957). Because of their small size and high energy requirements, hummingbirds probably accumulate such relatively large amounts of fat over several days. Migrating rufous hummingbirds (*Selasphorus rufus,* 3.5 g), which increase in mass 0.23–0.30 g d^{-1} during stops along their migration, must feed for 5 d or more before gaining enough mass to continue migration (Carpenter, Paton, and Hixon 1983; Carpenter and Hixon 1988). Carpenter and Hixon (1988) suggest that, in order to gain mass at this rate, hummingbirds must utilize torpor; otherwise a large portion of the fat stored during the day would be consumed at night. If so, the daily mass increases observed in *S. rufus* might represent the maximum net fat storage rate attainable. Because both species I studied remained in mass balance during metabolic trials (initial and final masses were not significantly different; tables 1, 2), daytime mass gain is equal to overnight mass loss. The daytime mass gains of *C. anna* and *C. costae* are, therefore, 0.69 g and 0.53 g, respectively (computed from data for overnight mass loss in tables 1 and 2), which are similar to that reported for *S. rufus* (0.50 g; Carpenter and Hixon 1988). If body composition of the birds in this study is similar to that of *S. rufus,* then fat-accumulation rates might be similar as well. Because of their high metabolic rates hummingbirds and other small birds might need to maximize the rate at which fat is stored if they are to meet their nocturnal energy demands. Daytime RQ of both *C. anna* and *C. costae* was well above 1.0 throughout the day, and, although this does not quantify fat-storage rate, it does indicate continuous fat synthesis (Kleiber 1975), which might be expected for an animal trying to maximize its fat stores.

Overnight mass loss results from oxidation of metabolic substrates, evaporative water loss, and evacuation of gut contents (King 1972). Mass changes due to oxidation result from differences in the mass of O_2 consumed and the mass of CO_2 produced (Kleiber 1975). On the basis of mean nighttime RQ and metabolic rate (table 1), oxidation accounts for only 14.3% (0.09

g) of the overnight mass loss in *C. anna* and 14.0% (0.07 g) of the overnight mass loss in *C. costae.* The remainder of the overnight mass loss can be accounted for by evaporative water loss, which is predicted to be 0.53 g for *C. anna* and 0.48 g for *C. costae* (Crawford and Lasiewski 1968; equation for birds at 25°C. I assume the difference in evaporative water loss at 25°C and 28°C is small.) Total overnight mass loss predicted from the combined effects of oxidation and evaporation is 0.62 g for *C. anna* and 0.55 g for *C. costae,* which are 10.1% and 3.8%, respectively, lower than the observed overnight mass loss. A portion of overnight mass loss might be due to defecation. However, overnight measurements of mass in individual birds show no evidence of defecation. This differs from the continuous mass measurements of hummingbirds by Beuchat et al. (1979) that suggest a significant mass loss occurs during the first hour after lights out, presumably because of defecation. Crop and gut contents, which are primarily water, might have been absorbed to replace water lost by evaporation. Sugar in the crop and gut was undoubtedly absorbed and metabolized.

Balancing the Energy Budget

The high nighttime RQs exhibited by *C. anna* and *C. costae* indicate that carbohydrate satisfied approximately half their nighttime energy demands. With the exception of *C. costae* during hours 16–17, the hummingbirds in this study did not rely totally on fat for energy at night. The preferential use of carbohydrate by birds as a means of conserving fat is known in nature. During their premigratory period, rosy pastors (*Sturnus roseus*) metabolize glycogen at night, ostensibly to save fat stores for migration (Pilo and George 1983). Whether the use of glycogen as a nighttime energy source by *S. roseus* is a unique adaptation is unclear because measurements of whole-body glycogen and its utilization are virtually nonexistent for other small birds. Mass-specific glycogen levels in *S. roseus* are, however, two to three times those of the American goldfinch (*Carduelis tristis;* Carey et al. 1978), the only other small bird for which whole-body glycogen has been determined.

Calypte anna and *C. costae* probably did not utilize glycogen as their primary carbohydrate source during the night in this study. To account for their observed nighttime RQs the hummingbirds would have to metabolize over 200 mg of glycogen (assuming 16.7 kJ g^{-1} glycogen as catabolizable energy; Kleiber 1975). If hummingbirds are similar in body composition to *S. roseus,* they would contain < 10 mg of glycogen, only 5% of the amount required to produce the observed nighttime RQs. A more likely source of carbohydrate for hummingbirds is sugar stored in the crop prior to the noc-

turnal fast. The mean predicted crop volume of *C. anna* is 0.65 mL (Hainsworth and Wolf 1972). A crop this size could hold 0.16 g of sucrose (0.25 g sucrose mL^{-1} feeder solution), which supplies 2.7 kJ (assuming 16.7 kJ g^{-1} sucrose as catabolizable energy; Kleiber 1975). Predicted mean crop volume for *C. costae* is 0.59 mL (Hainsworth and Wolf 1972). A crop this size could hold 0.15 g sucrose, which supplies 2.5 kJ. For both species this amount of carbohydrate could account for the observed RQs, if the birds anticipated the end of the day and filled their crop before the lights were turned out (table 4). Because the sugar stored in the crop can provide up to 50% of their nighttime energy needs, hummingbirds could remain normothermic at night and still conserve a large portion of their lipid reserves.

I was unable to examine the crops of the birds during the metabolic measurements. Some birds increased their rate of mass gain during the few hours prior to the dark phase, possibly from crop filling. However, an examination of the average rate of hourly mass gain shows no significant increase and a high degree of variability (fig. 4). Because I measured hourly mass averages, increases in mass of individual birds due to feeding might not be detected if the birds also defecated during the hour. In addition, it is possible that crop filling in some birds began earlier in the day because of the absence of a visual cue marking the onset of the dark phase. Flight activity does appear to increase slightly a few hours before the beginning of the dark phase (fig. 5), but these data are variable as well and the increase in flight activity is not statistically significant.

Caged hummingbirds (n = 7) that I examined immediately after lights off at night appeared to have full crops. This indicates that crop filling prior to the nocturnal fast for these caged birds is anticipatory, because hum-

TABLE 4

Comparison of observed respiratory quotient (RQ) to RQ predicted if sugar stored in the crop is metabolized at night

Species	Predicted Crop Volume (mL)[a]	Energy in Crop (kJ)[b]	Nighttime Energy Cost (kJ)	Nighttime RQ	
				Predicted	Observed
Calypte anna	.66	2.7	6.8	.83	.88
Calypte costae	.58	2.4	5.7	.83	.85

[a] Crop volume (mL) = 0.206 × mass (Hainsworth and Wolf 1972).

[b] Energy in crop = crop volume (mL) × 0.25 g sucrose/mL × 16.7 kJ/g sucrose.

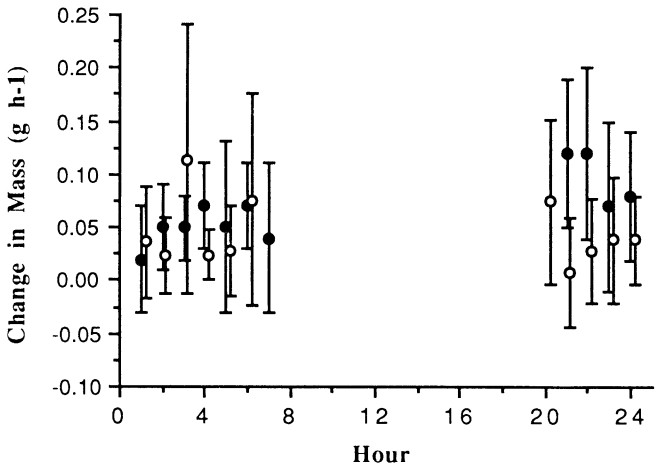

Fig. 4. Net change in mass during each hour of the light phase. Vertical bars represent ± 1 SD of the mean. Filled circles represent Calypte anna; *empty circles represent* Calypte costae.

mingbirds rarely fill their crops while feeding during the day (DeBenedictis et al. 1978; Hainsworth 1978). Anticipatory crop filling by hummingbirds is consistent with previous observations of feeding behavior in captive hummingbirds (Beuchat et al. 1979; Tiebout 1989) and free-living *C. anna* (Wheeler 1980).

When hummingbirds anticipate the onset of the nocturnal fast by filling their crops with sucrose solution, RQ declines slowly throughout the night

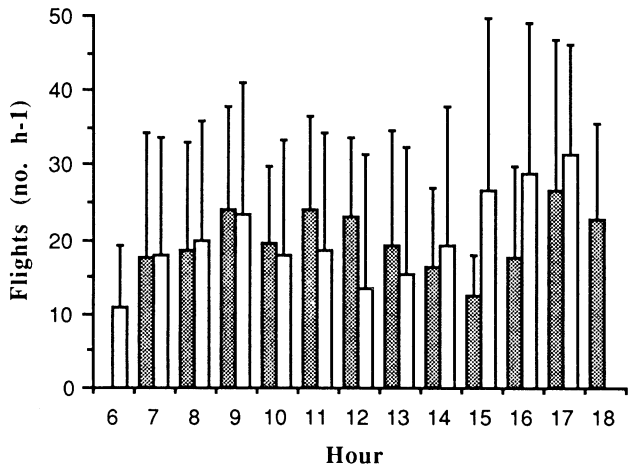

Fig. 5. Total number of flights during each hour of the light phase. Vertical bars represent ± 1 SD of the mean. Shaded squares represent Calypte anna; *empty squares represent* Calypte costae.

(fig. 3). This supports the data of Tiebout (1989) that suggest roosting hummingbirds lower their crop-emptying rates. When food is abruptly withdrawn, gut sucrose reserves are low and RQ declines more rapidly. To illustrate this, I removed fed *C. anna* from their cages at midday and measured their respiratory gas exchange. After 2 h without feeding, RQ averaged 0.79 ± 0.02, whereas RQ was 0.95 ± 0.08 at 2 h into the dark period during the 24-h metabolic trials. These values are significantly different ($t = 4.74$, df = 13). This suggests that hummingbirds become "postabsorptive" more quickly when fasted during their active phase, because their crop is not as full and they are therefore not prepared for a long-term fast.

Use of the crop as a nighttime "storage depot" is suggested by observations of bimodal feeding patterns in free-living hummingbirds. Feeding activity in free-living hummingbirds is most intense in the morning when the crop is presumably empty, declines during midday, and increases again at the end of the day (Wheeler 1980). This end-of-day feeding burst may represent the hummingbird's effort to "top off the tank" before going to roost. Volume of the crop thus might act as the "fuel gauge" hypothesized by Calder and Booser (1973) and could trigger torpor or, perhaps, provide input to regulatory mechanisms that adjust the degree of hypothermia (Hainsworth and Wolf 1970).

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