FIELD METABOLIC RATE AND FOOD CONSUMPTION OF TWO SYMPATRIC HUMMINGBIRD SPECIES IN SOUTHEASTERN ARIZONA[1]

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Abstract. We compared the field metabolic rate (FMR) and behavior around sugar-water feeders of sympatric territorial and non-territorial hummingbirds in the Chiricahua Mountains of southeastern Arizona during July 1987 and 1989. The territorial species was the Blue-throated Hummingbird (*Lampornis clemenciae*; mean mass 8.77 g) and the non-territorial species the Black-chinned Hummingbird (*Archilochus alexandri*; mean mass 3.67 g). FMR (CO_2 production) and water turnover were measured using the doubly labeled water technique. FMR averaged 81.7 kJ/day ($n = 4$) in *L. clemenciae* and 29.1 kJ/day ($n = 4$) in *A. alexandri*. Mean mass-specific FMR was higher in *L. clemenciae* (18.36 ml CO_2 g^{-1} hr^{-1}) than in *A. alexandri* (15.58 ml CO_2 g^{-1} hr^{-1}). This might be due to higher activity costs associated with the aggressive territorial behavior of *L. clemenciae*. Water influx averaged 1,734 ml kg^{-1} day^{-1} in *L. clemenciae* ($n = 5$) and 1,728 ml kg^{-1} day^{-1} in *A. alexandri* ($n = 6$). These values represent turnover rates equivalent to 185% and 245% of body mass per day respectively and are consistent with measurements made on other hummingbird species. Where these species coexist in the Chiricahua Mountains, *L. clemenciae* is a dominant territorial species whereas *A. alexandri* appears to be non-territorial, acquiring energy by robbing nectar from *L. clemenciae* territories. *Lampornis clemenciae* is highly aggressive against conspecifics, but appears to ignore intruding *A. alexandri*. Lack of territorial defense behavior in *A. alexandri* might reduce field energy expenditures and contribute to a lower FMR than *L. clemenciae*. We hypothesize that the lack of territorial aggression by *L. clemenciae* against *A. alexandri* is due to the high quality, abundance, and predictability of their food source which eliminates the profitability of such aggression. We also suggest that the intense aggression exhibited by *L. clemenciae* towards conspecifics might be motivated by factors relating to fitness other than defense of a food source.

Key words: Doubly labeled water; Archilochus alexandri, Lampornis clemenciae*; Trochilidae; energetics; water turnover; territoriality.*

INTRODUCTION

Variation in FMR and water turnover can reflect differences in overall activity patterns between individuals. For example, many hummingbirds defend feeding territories making frequent short flights to forage, chase intruders, and to perform aggressive displays (Hainsworth and Wolf 1971, Stiles 1971, Kodric-Brown and Brown 1978, Ewald and Bransfield 1987). Because flight is an energetically expensive activity (Bartholomew and Lighton 1986), chases and displays can contribute significantly to FMR. Other hummingbird species are non-territorial, and rarely engage in defensive behaviors. A greater percentage of FMR might be attributable to flight costs due to an increased difficulty in finding food, an increase in the amount of time required to travel between

dispersed food sources, and chases initiated by territory owners (Wolf 1978). Examples of non-territorial hummingbirds include subordinate species that are excluded from food sources in a given area (e.g., Pimm et al. 1985), and traplining species that forage over a wide area (Stiles and Wolf 1979, Feinsinger 1986). Although attempts have been made to estimate the relative energy cost associated with these different foraging methods (Schoener 1971, Carpenter and MacMillen 1976, Wolf 1978, Hixon et al. 1983), few empirical data are available on non-territorial hummingbirds making direct comparisons with territorial species difficult. In addition, comparisons are complicated by differences in the climatic factors (such as radiation, wind, and humidity) experienced by individual species which can have a significant impact on FMR (e.g., Bakken 1976).

The Black-chinned Hummingbird (*Archilochus alexandri*, about 3.5 g) and the Blue-throated Hummingbird (*Lampornis clemenciae*, about

8.5 g) are sympatric in the Chiricahua Mountains of southeastern Arizona. Pimm et al. (1985) showed that the foraging behavior of *A. alexandri,* typically a territorial species (e.g., Ewald and Bransfield 1987), is radically altered by interference competition from the larger and highly territorial *L. clemenciae. Lampornis clemenciae* can prevent *A. alexandri* from defending "good" food patches, forcing them to become non-territorial and forage only at "poorer" food patches or rob nectar from *L. clemenciae* territories. The energetic consequence of this interaction for both *A. alexandri* and *L. clemenciae* is unclear.

To determine whether a territorial or non-territorial foraging method is energetically more expensive, we measured FMR in free-living *L. clemenciae* and *A. alexandri* using the doubly labeled water (DLW) technique (Lifson and McClintock 1966, Nagy 1980, Nagy and Costa 1980) in conjunction with time-budget analysis and feeding rate measurements. Although important behavioral information can be obtained from time budgets, the DLW method is necessary to measure FMR in hummingbirds because time-budget analysis on non-territorial species is difficult, and because substantial errors can result from indirect estimates of FMR based on time budgets alone if the thermal environment is not correctly assessed (Weathers et al. 1984). In addition to providing a direct measurement of FMR, the DLW method also provides an estimate of water turnover rate, which in turn can be used to estimate feeding rate, especially in nectarivores for whom water intake and foraging are tightly coupled (Powers and Nagy 1988).

MATERIALS AND METHODS

STUDY AREA

We conducted the field portions of this study on post-breeding birds during July 1987 (DLW) and 1989 (time budgets) at the American Museum of Natural History's Southwestern Research Station in the Chiricahua Mountains, Cochise County, Arizona (latitude 31°50′N, longitude 109°15′W; 1,700 m altitude). The riparian habitat surrounding the station is bordered by oak woodland and a mixed deciduous/coniferous forest. Four potential territory sites were identified and supplied with feeders containing a 25% sucrose solution (1.0 g sucrose mixed with 3.0 g water). Food was available ad libitum. We used 12 ml syringes with regular Luer tips (Monoject

#512910) as feeders. The tips of the syringes were cut off to slightly enlarge the hole and painted red with nail polish. Each potential territory location was supplied with four syringes inserted through a plexiglas plate suspended from an aluminum pole. Feeder locations were approximately 100 m apart. Small insects of a size presumably suitable as hummingbird prey were abundant during the study.

DOUBLY LABELED WATER

We measured FMR and water turnover in free-living Blue-throated Hummingbirds (*Lampornis clemenciae*) and Black-chinned Hummingbirds (*Archilochus alexandri*) using the doubly labeled water technique (Lifson and McClintock 1966, Nagy 1980, Nagy and Costa 1980) in 1987. To minimize trauma to the birds, we used the single sample method (Nagy et al. 1984, Webster and Weathers 1989). Birds were captured with mist nets (Arizona Game and Fish permit #00006; Federal Fish and Wildlife permit #PRT-694387), weighed to the nearest 0.05 g with a K-Tron model DS-10 electronic balance, given a unique color marking on the back with model airplane paint. They were then given an injection in the pectoralis muscle of 35 μl (*A. alexandri*) or 70 μl *L. clemenciae*) of water (containing 70 μCi of tritium and 95 atoms percent oxygen-18) with a 50 or 100 μl Hamilton microliter syringe, and released. Birds were recaptured approximately 24 hr later, reweighed, and a 50–80 μl blood sample collected by toe clipping. Blood samples were collected in heparinized microhematocrit tubes, flame sealed, and stored at 4°C. They were later transported on ice to the University of California, Davis, for analysis. Three additional birds were sampled but not injected to measure background levels of isotope in the blood.

ISOTOPE ANALYSIS

Blood samples were microdistilled under vacuum to yield pure water, which was analyzed for tritium content by liquid scintillation, and for oxygen-18 content by proton activation (Wood et al. 1975). Rates of CO_2 production and water flux were calculated using the equations for linearly-changing body water volumes (Nagy 1980, Nagy and Costa 1980). Total body water was determined by sacrificing the birds at the time of recapture and drying them at 67°C to a constant mass (3–4 days). Initial equilibrium isotope levels were estimated from a separate control

group of eight birds (4 *L. clemenciae* and 4 *A. alexandri*). These birds were processed as follows: (1) captured and injected as described above, (2) held for 1 hr, (3) weighed to the nearest 0.01 g, and (4) a blood sample taken. They were then sacrificed and dried to constant mass. We assumed that the isotope ratio (ln $^3H/^{18}O$) for each of the experimental birds was equal to the mean isotope ratio of the control birds, and used this ratio in our calculations of FMR (Webster and Weathers 1989). Initial tritium activity (^3H_i) was predicted from the equation $^3H_i = C_H/TBW_i$, where TBW_i is the initial TBW estimated from the control birds [H_2O (g)/live mass (g)] and C_H is a constant calculated from initial tritium activities in the control birds [^3H specific activity $\times$ TBW (g)] that incorporates the tritium specific activity of the injection solution and the dose (Nagy et al. 1984). These values were used in our calculations of water influx.

TIME BUDGETS

Although time budgets are limited in their usefulness for direct calculation of energetic costs in this type of study, they can provide important behavioral information that can aid in the interpretation of the DLW results. We conducted observations on territories established around each of the experimental feeders in 1989. Feeder locations in 1989 were placed in the same locations as in 1987. Observations were conducted for 1-hour intervals between 05:00 hr and 19:00 hr (the range of times over which hummingbirds were active). For convenience observation periods always started on the hour. A total of 60 hr of time budget were collected each for *L. clemenciae* and *A. alexandri*. Observation time for *L. clemenciae* was divided among the territory owners in approximately equal amounts, whereas observations for *A. alexandri* involved several individual birds. During each observation period an observer (either Powers and Conley) was positioned approximately 20 m from the territory feeder. Observation schedules were determined in advance with time, territory, and observer selected randomly. The observer recorded frequency and duration of activities for both *L. clemenciae* and *A. alexandri*. Activities timed for *L. clemenciae* were perching, nectar feeding, chasing, miscellaneous flight, and out-of-sight. Chasing was subdivided into two categories: intraspecific and interspecific. Miscellaneous flight was defined as flight around the territory for which

we could not determine a purpose. Flycatching was included in miscellaneous flight because it constituted only a small portion of *L. clemenciae*'s daily activity. Out-of-sight time (OOS) included periods when the territory owner was off the territory or not observed. Timed observations for *L. clemenciae* were recorded with a TRS 100 lap-top computer (Tandy Corp.). Activities recorded for *A. alexandri* were nectar feeding and chasing. Chases were separated into those in which *A. alexandri* was the aggressor and those in which *A. alexandri* was being expelled from the territory. Timed observations for *A. alexandri* were recorded using stop watches.

TOTAL FOOD CONSUMPTION

To track feeding patterns and total daily food consumption from each experimental feeder, changes in feeder volume were recorded each hour (05:00 hr to 19:00 hr) to the nearest 0.2 ml. The volume of syringes used as experimental feeders were calibrated by weight to improve the accuracy of our volume measurements. Feeders were filled at the beginning of each day before the hummingbirds were active, and the final feeder measurement occurred after the hummingbirds went to roost.

FEEDING RATE

To determine the energetic benefits received by each hummingbird species from a given territory we needed a measure of feeding rate that could be converted to energy consumed during a feeding bout. Feeding rate was determined by measuring the mass of feeder solution removed by a hummingbird during a feeding bout over time. Feeder mass was measured using a calibrated strain gauge (measurements Group, Inc. EA-06-125B2-350) attached to a brass beam from which the feeder was suspended. Mass measurements were accurate to 0.01 g. The strain gauge was calibrated by hanging precision weights from the beam. Output from the strain gauge was sampled at 0.5 sec intervals with a Campbell Scientific CR21X data-logger. Data from the CR21X were then analyzed using a Macintosh Plus computer. Because of the special nature of this apparatus feeding rate measurements had to be made at a location near our laboratory.

METEOROLOGICAL MEASUREMENTS

We characterized the thermal environment, which can significantly impact FMR (Bakken

1976), with standard meteorological measurements collected each day of the study in an unsheltered area near the research station 3 m above the ground. Ambient temperature (T_a) in the shade was measured with a 24-gauge Cu-Cn thermocouple, operative temperature (T_e; Winslow et al. 1937) with a copper sphere thermometer painted flat-gray (Walsberg and Weathers 1986), wind speed with a Thornthwaite model 901-LED cup anemometer, and relative humidity with a Campbell Scientific model 207 temperature and relative humidity probe. Output from each measurement device was sampled every minute and averaged every 15 min by a Campbell Scientific CR21X Micrologger. We measured precipitation with a rain gauge maintained by the station. All measurements were made continuously (24 hr/day) throughout the study (16–29 July 1987 and 5–20 July 1989).

STATISTICS

Correlations were determined by linear least-squares regression (Zar 1974). Results are given as the mean ± one standard deviation. Statistical significance was assumed if $P < 0.05$.

RESULTS

DOUBLY LABELED WATER

We injected and released 27 experimental *Lampornis clemenciae* (mean mass 8.34 ± 0.69 g) and 33 experimental *Archilochus alexandri* (mean mass 3.69 ± 0.40). Of these released experimental birds, we recaptured eight *L. clemenciae* (four after 24-hr) and nine *A. alexandri* (four after 24-hr). One *A. alexandri* was recaptured in less than one day with its measurement interval confined to the active period. Birds recaptured after more than one day generally did not contain sufficient oxygen-18 for CO_2 analysis. Three birds recaptured after more than one day did have enough tritium remaining to calculate water flux, however.

Mean mass for the *L. clemenciae* control group ($n = 4$) was 8.30 ± 0.34 g, and total body water (TBW) volume was 5.60 ± 0.45 ml (67.5% of total mass). For the experimental *L. clemenciae* group ($n = 5$), initial mass and total body water (TBW_i) volume was 8.64 ± 0.64 g and 5.80 ± 0.39 ml (estimated assuming initial TBW fraction = final TBW fraction), respectively. Initial mass and TBW of the experimental group did not differ significantly from the mass and TBW

of the control group (for mass $t = 1.6$, df = 7, ns; for TBW $t = 0.47$, df = 7, ns). Final mass and TBW volume (TBW_f) for *L. clemenciae* were 8.85 ± 0.64 g and 5.95 ± 0.39 ml (67.2% of total mass) respectively. For *A. alexandri,* mass and TBW volume for the control group ($n = 4$) were 3.61 ± 0.23 g and 2.36 ± 0.35 ml (65.4% of total mass), respectively. Initial mass and TBW_i for the experimental group ($n = 6$) were 3.73 ± 0.19 g and 2.47 ± 0.12 ml (estimated from measurements of final TBW). Initial mass and TBW of the experimental group did not differ significantly from the control (for mass $t = 0.14$, df = 8, ns; for TBW $t = 0.68$, df = 8, ns). Final mass and TBW_f were 3.56 ± 0.55 g and 2.36 ± 0.35 ml (66.3% of total mass).

Mean log isotope ratios (ln $^3H/^{18}O$) for *L. clemenciae* and *A. alexandri* were −11.2492 (range: −11.2074 to −11.3314) and −11.2446 (range: −11.2063 to −11.3108), respectively. Mean C_H was 299,584 (range: 276,203 to 329,899) for *L. clemenciae* and 201,295 (range: 195,483 to 209,218) for *A. alexandri.* Isotope background values were 0.2032 atom% for oxygen-18 and 49 CPM for tritium.

Mean FMR was 18.36 ± 1.85 ml CO_2 g^{-1} hr^{-1} for *L. clemenciae* and 15.58 ± 2.44 ml CO_2 g^{-1} hr^{-1} for *A. alexandri.* From these values we estimated FMR to be 81.7 ± 11.0 kJ/day for *L. clemenciae* and 29.1 ± 6.3 kJ/day for *A. alexandri* (assuming 21.1 kJ/l CO_2 for a carbohydrate diet). For the one *A. alexandri* measured during the active phase alone, FMR was 25.16 ml CO_2 g^{-1} hr^{-1}. FMR data for individual birds are summarized in Table 1.

Mean water influx for *L. clemenciae* was 15.18 ± 2.04 ml/day (1,734 ml kg^{-1} day^{-1}). *Lampornis clemenciae* generally gained mass during this study. Mean water influx for *A. alexandri* was 6.18 ± 0.79 ml/day (1,728 ml kg^{-1} day^{-1}). *Archilochus alexandri* generally lost mass during this study. Water flux and body mass data are summarized in Table 1.

TIME BUDGETS

Data for each territory are presented in Table 2. Territory owners were either not visible or off their territories for an average of about 60% of the time. Because territorial *L. clemenciae* often perched high in trees where they were difficult to see, we suspect that territorial males were simply perched during much of the recorded OOS time. While observed on their territory, *L. clemenciae*

TABLE 1. Field metabolic rate and water turnover of free-living *Archilochus alexandri* and *Lampornis clemenciae*.

Bird no.	Body mass		Time (days)	FMR[1]		Water influx	
	$\bar{x}$ (g)	% change		ml CO_2 g^{-1} hr^{-1}	kJ/day[2]	ml kg^{-1} day^{-1}	ml/day
			Archilochus alexandri (24–hr)				
4	3.53	−16.9	0.84	13.08	23.4	1,711	6.1
10	3.30	−8.7	1.12	16.96	28.3	2,222	7.3
26	3.75	−5.3	0.99	14.01	26.6	1,305	4.9
33	3.33	−7.3	0.86	—	—	1,922	6.4
34	3.68	−11.5	0.95	—	—	1,732	6.4
35	4.10	13.0	0.89	18.27	37.9	1,481	6.1
$\bar{x}$	3.62	−6.1	0.94	15.58	29.1	1,729	6.2
SD	0.30	10.2	0.10	2.44	6.3	323	0.8
			Archilochus alexandri (daytime)				
9	3.55	5.8	0.34	25.16	45.2	1,491	5.29
			Lampornis clemenciae (24–hr)				
1	8.45	−3.5	1.02	18.42	78.8	1,742	14.7
4	8.85	−2.2	1.07	—	—	1,540	13.6
6	9.58	2.7	1.15	18.10	87.8	1,431	13.7
8	8.23	8.2	1.15	16.20	67.5	1,846	15.2
11	8.83	2.9	0.86	20.71	92.6	2,110	18.6
$\bar{x}$	8.77	2.6	1.05	18.36	81.7	1,734	15.2
SD	0.59	4.8	0.14	1.85	11.0	266	2.0

[1] *Archilochus alexandri* numbers 33 and 34, and *Lampornis clemenciae* number 4 were omitted from mean and standard deviation calculations.
[2] Assuming 21.1 kJ/L CO_2 for a carbohydrate diet.

perched approximately 70% of the time. Thus, more intense activity was confined to only a few minutes during an hour-long time budget. Likewise, total feeding time per hour was generally less than 1 min. Territory owners feed on average eight times per hour (range 0 to 17) with each feeding bout lasting an average of 6 ± 2 sec. Activity showed no clear temporal pattern. Feeding time does exhibit possible bimodal activity (as might be expected for hummingbirds; see Calder et al. 1990) with the highest feeding times being in the evening just prior to going to roost, but the high variability in the measurements make any suggested differences insignificant.

Intraspecific intruders were chased almost without exception. During this study male *L. clemenciae* were rarely able to feed unmolested at a territory owner's feeder. Territory owners con-

fronted 93.3% of the intraspecific intruders (642/688). At no time was a territory owner observed to be displaced as a result of an intraspecific confrontation. Chases of intraspecific intruders were often complex, sometimes involving up to three intruding individuals. In contrast, interspecific intruders (primarily *A. alexandri*) were rarely chased. During the study we observed *A. alexandri* being chased from a territory by an *L. clemenciae* male only 11.7% (59/504) of the time. In addition, *A. alexandri* fed regularly at the territory feeder defended by *L. clemenciae*, usually while the territory owner was away. Often as many as four *A. alexandri* would feed from a territorial feeder simultaneously. When *A. alexandri* was present at the feeders in groups, we often observed aggression between individuals. Aggression between *A. alexandri* at the feeders

TABLE 2. Time budget data for territorial *Lampornis clemenciae*. Values are expressed as $\bar{x}$ (min/hr) ± 1 SD.

Territory	Perching	Chasing	Feeding	Misc. flight	OOS
A	23.5 ± 13.0	3.1 ± 2.8	1.0 ± 0.6	4.7 ± 3.1	25.1 ± 16.3
B	20.0 ± 18.9	1.0 ± 1.2	0.8 ± 0.5	2.2 ± 2.1	34.5 ± 20.4
C	14.3 ± 13.8	1.7 ± 1.9	0.6 ± 0.5	2.4 ± 1.9	39.4 ± 16.4
D	10.5 ± 13.4	1.9 ± 3.1	0.9 ± 0.6	1.5 ± 1.1	44.0 ± 15.8

lasted only a few seconds and did not appear to hinder the ability of individual *A. alexandri* to feed.

FOOD CONSUMPTION

Mean total daily food consumption at individual territories was: 46.7 ± 16.5 ml/day in territory A, 64.7 ± 22.7 ml/day in territory B, 52.8 ± 13.7 ml/day in territory C, and 67 ± 38.4 ml/day in territory D. The smallest amount of food removed by hummingbirds in a single day was 18.2 ml from territory D, and the most food removed was 127.8 ml, also from territory D. Day-to-day food consumption was highly variable in all territories.

FEEDING RATE

Feeding rate was highly variable. Male *L. clemenciae* consumed 1.30 ± 1.04 g/min of feeder solution ($n = 16$ birds), whereas *A. alexandri* consumed 0.51 ± 0.15 g/min of feeder solution ($n = 11$ birds). When feeding, hummingbirds often paused for one to several short periods during the feeding bout (<1 sec in duration). This is a potential source of error for these measurements. The magnitude of this error is, however, unknown because these pauses are also exhibited by hummingbirds feeding in the wild (personal observation) and are thus a normal part of feeding behavior. The frequency of pauses during a feeding bout is generally higher for *A. alexandri* than for *L. clemenciae*. These measurements should be considered only first approximations.

WEATHER

The monsoon season, a period of frequent and often heavy rainfall, is usually well under way by July in southeastern Arizona. However, 1987 was a particularly dry year with total daily rainfall greater than 0.1 cm occurring on only five days during the study (maximum 2.36 cm, July 28). Cloud cover was present on each day, but was variable throughout the day. Maximum ambient temperature (T_a) averaged 32.23 ± 4.00°C and minimum T_a averaged 14.58 ± 2.23°C. T_a reached its maximum at 15:00 hr and its minimum at 07:00 hr. Maximum operative temperature (T_e), the sum of T_a and a temperature increase or decrease due to radiative and convective factors (e.g., Bakken 1976), averaged 33.96 ± 4.18°C and minimum T_e 14.69 ± 2.20°C. T_e was slightly higher than T_a from 12:00 hr to 15:00 hr

but these differences were small. Wind speed was highly variable, averaging between 1.0 m/sec and 2.0 m/sec during the day and less than 1.0 m/sec at night. Relative humidity (RH) averaged about 18% (about 6.0 g of water/m³) during the day and about 22% (about 3.0 g of water/m³) at night.

Weather conditions in 1989 were roughly similar to those in 1987. In 1989 rainfall occurred more frequently, with total daily rainfall exceeding 0.1 cm on 18 days (maximum 1.85 cm, July 20). As in 1987, cloud cover was present during portions of each day, but variable throughout the day. Maximum T_a averaged 31.5 ± 3.3°C and minimum T_a averaged 12.3 ± 1.8°C. Maximum T_a occurred at 16:00 hr and minimum temperature occurred at 06:00 hr. Maximum T_e averaged 35.9 ± 4.7°C and minimum T_e averaged 12.0 ± 1.9°C. Maximum T_e occurred at 15:00 hr and minimum T_e occurred at 06:00 hr. T_e was typically 3 to 5°C higher than T_a between 08:00 hr and 17:00 hr (mean difference = 4.09 ± 0.78°C). Wind speed was consistent at about 0.75 m/sec throughout the study, which is less than that recorded in 1987. Relative humidity averaged about 19% during the day (about 6.0 g of water/m³) and 22% (about 2.5 g of water/m³) at night.

DISCUSSION

FIELD ENERGY EXPENDITURE

Field metabolic rate measurements have shown that hummingbirds are "hard working" (see Weathers and Stiles 1989 for discussion). The birds measured in this study were no exception. The FMR of *L. clemenciae* and *A. alexandri* are 87% and 17% respectively higher than allometric predictions (Nagy 1987). In addition, the ratio of FMR to resting metabolic rate (relative power requirement, King 1974) for *L. clemenciae* was 8.0 (assuming resting metabolic rate = 2.3 ml O₂ g⁻¹ hr⁻¹, Lasiewski and Lasiewski 1967), one of the highest measured for any bird (see Weathers and Sullivan 1989). Weathers and Stiles (1989) caution that estimates of the relative power requirement of hummingbirds might be unrealistically high, however, because we do not know their true nighttime resting metabolic rate (see Powers 1992 for discussion). Even so, these data underscore the high energy demands faced by hummingbirds.

We compared our FMR measurements from DLW to estimates of energy intake calculated

TABLE 3. Field metabolic rate of hummingbirds measured with doubly-labeled water.

Species	Mass (g)	n	FMR (kJ/day)	Source
Archilochus alexandri	3.67	4	29.1	This study
Calypte anna	4.48	8	31.8	Powers and Nagy (1988)
Thalurania colombica	4.91	9	37.9	Weathers and Stiles (1989)
Chalybura urochrysia	7.18	1	57.9	Weathers and Stiles (1989)
Lampornis clemenciae	8.77	4	81.7	This study

from measures of feeding rate. *Lampornis clemenciae* consume 1.3 g/min of sucrose solution (0.325 g sucrose/min) and foraged an average of 0.81 ± 0.57 min/hr (Table 2). Based on these values *L. clemenciae* consumes 60.8 ± 42.8 kJ/day (assuming 1 g sucrose = 16.5 kJ metabolizable energy; Weast et al. 1983). This is slightly more than 20 kJ less than our measurement of FMR for *L. clemenciae* using DLW. However, our DLW measurement falls well within 1 SD of the calculated energy intake. Thus, we have no reason to consider our DLW measurement to be inaccurate. We are unable to make a similar calculation for *A. alexandri* because we could not consistently track individual birds.

Comparing FMR data between hummingbird studies is difficult because of differences in day-length, weather, and body size. In this study, however, comparing data is easier because the two species presumably experienced the same weather conditions and photoperiod. Mass-specific FMR in *L. clemenciae* is still 18% higher than that of *A. alexandri* (Table 3) suggesting that *L. clemenciae* spends relatively more energy than *A. alexandri* on activity each day. This result is opposite of that predicted by all allometric models of FMR for birds (Walsberg 1983, Nagy 1987). One explanation for this is that food (energy) availability was unlimited. Thus, the high amount of energy devoted to activity by *L. clemenciae* could be supported by territorial resources. Alternatively, the high level of aggression exhibited by territorial *L. clemenciae* towards conspecifics could play some role in determining the fitness of the territory owner. Thus, the short-term energetic costs of this aggression are perhaps tolerated in exchange for long-term reproductive gains.

An examination of the available DLW data for other hummingbirds (five species including this study; Table 3) suggests that current allometric models for predicting FMR might be unreliable for use with hummingbirds, and that

larger hummingbirds might, in fact, have higher mass-specific FMRs than smaller hummingbirds. However, because this apparent trend is based on several studies involving small sample sizes, more work needs to be done before this relationship can be validated. If this trend is correct it might be because larger hummingbirds tend to be socially dominant, and thus might be more aggressive and active than smaller species. *Lampornis clemenciae* males, for example, actively exclude intraspecific intruders from their territories at the Southwestern Research Station (Pimm 1978, Pimm et al. 1985, this study). In addition, they presumably prevent *A. alexandri* from establishing territories, forcing them to become an intruding species. If the relative energy cost of excluding intruders from a food source is greater than the cost of being a territorial intruder, this could explain *L. clemenciae*'s higher mass-specific FMR. An alternative explanation for the above trend would be that smaller hummingbirds make more frequent use of torpor than larger species. However, if the FMR of the single *A. alexandri* we measured during daytime (Table 1) reflects that of the *A. alexandri* population, then nighttime energy expenditure would be about 3 to 4 kJ. This is 10 to 13 times higher than would be expected for *A. alexandri* entering torpor (0.03 kJ/hr; highest value reported by Lasiewski 1963). Another possible explanation for the observed differences in mass-specific FMR is that *L. clemenciae* and *A. alexandri* reacted differently to the stress of handling and injection. For example, handling stress might affect dominant and subordinate species differently because of their social status (Silverin et al. 1989) or because subordinate species, such as *A. alexandri*, are already under greater stress to begin with (Fretwell 1969). In any event if *A. alexandri* was stressed by the injection procedure to a greater degree than *L. clemenciae* then depressed levels of activity and food intake could be the result. A higher stress level in *A. alexandri* might be

indicated by the fact that most of the birds lost mass during the DLW experiments (Table 1).

WATER TURNOVER

The relatively high water flux exhibited by hummingbirds reflects their small size and liquid diet. For birds in this study, water influx averaged 1,728 ml kg^{-1} day^{-1} for *A. alexandri* and 1,734 ml kg^{-1} day^{-1} for *L. clemenciae* (Table 1). These values are greater than that of *C. anna* (1,640 ml kg^{-1} d^{-1} Powers and Nagy 1988), but less than that observed for *Thalurania colombica* and *Chalybura urochrysia* (2,392 ml kg $^{-1}$ day^{-1} and 2,001 ml kg^{-1} day^{-1} respectively; Weathers and Stiles 1989). These values are respectively 185% and 245% higher than predicted allometrically for birds (Nagy and Peterson 1988). Both *A. alexandri* and *L. clemenciae* turnover water equivalent to 173% of their body mass per day.

SOCIAL INTERACTIONS

Non-territoriality probably offers *A. alexandri* a greater net energetic benefit than would be attained by competing directly with *L. clemenciae* or defending an inferior food source (Gill and Wolf 1975, Carpenter and MacMillen 1976, Ewald and Carpenter 1978, Gill 1978, Wolf 1978). We observed *A. alexandri* visiting *L. clemenciae* territories at regular intervals. The few individuals that we could consistently identify returned to a territory about every 15 min. After arriving at the territory they would perch several meters from the feeder and wait for the territory owner to leave, after which they would feed. Because *A. alexandri* feed primarily when *L. clemenciae* are absent from the territory, the high cost of being chased is avoided. In addition, *A. alexandri* are able to exploit a predictable and abundant food source without the high cost of defending it. For example, about 67 ml/day of nectar was consumed from territory D. This is equal to 306 kJ (assuming 1.0 ml of 25% sucrose solution contains 0.277 g of sucrose and 1.0 g sucrose is equal to 16.5 kJ metabolizable energy; Weast et al. 1983). If *L. clemenciae* FMR is 82 kJ/day, then 224 kJ more than what is required by the territory owner has been consumed from the feeders at territory D (assuming 100% digestive efficiency). This amount of energy would support the daily energy requirement of more than seven *A. alexandri*. Similar calculations for territory A, the territory with the lowest average nectar consumption per day, suggest that more than four *A. alexandri* could be supported.

Alternatively, the excessive energy removal from territorial feeders could be explained if intruding *L. clemenciae* were able to feed successfully. Although we did not see intruding *L. clemenciae* feed very often, we did not watch each territory continuously throughout the day. We estimate from time budgets and feeding rate measurements that *L. clemenciae* (including intruders) were in fact responsible for an average of 57% (152 kJ) of the total energy removal from the territories. This is slightly less than two times our 1987 DLW measurement of *L. clemenciae* FMR.

Even though *L. clemenciae* feeding was responsible for the majority of energy removal from the territories, the total amount of energy consumed was in large part dependent upon the level of *A. alexandri* intrusion. A regression of the total amount of nectar removed from territories each day on the feeding rate (min/hr) of each species shows that the amount of time spent feeding by *L. clemenciae* explained only 14% of the variability in nectar removal (y = 41.65 + 16.83x, $r^2 = 0.14$). The feeding rate of *A. alexandri*, however, explained 46% of the variation in nectar removal from the feeders (y = 41.98 + 13.09x, $r^2 = 0.46$). Thus, *A. alexandri* appear to have a much greater impact on total feeder depletion than do *L. clemenciae*. Also, the energy consumed each day by *L. clemenciae* can support a maximum of two individuals (the territory owner and perhaps a single intruder) whereas the energy consumed by *A. alexandri* can support at least 4 individuals.

The social systems of various hummingbirds have been shown to be strongly influenced by the quality and distribution of a food source (e.g., Stiles 1971, Powers 1987). We believe that the characteristics of the food source affected *L. clemenciae* and *A. alexandri* behavior as well. In this study food was available, abundant, and concentrated throughout the day. Because the territory owners had presumably become conditioned to the reliability of this food source, the urgency to protect an accumulating nectar supply might have been nonexistent. In essence, the profitability of excluding *A. alexandri*, as well as other interspecific intruders, might have been eliminated. As for intraspecific aggression, it is likely that competition for a food source is only one reason for this aggression. *L. clemenciae* males might also be engaged in such things as reproductive behavior (although both species appeared to be post-breeding) or the establishment

of social ranking which could require aggression to continue regardless of the condition of the food resource. We are currently examining the impact of energy availability on territorial aggression in a separate study.

ACKNOWLEDGMENTS

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