Influence of Normal Daytime Fat Deposition on Laboratory Measurements of Torpor Use in Territorial versus Nonterritorial Hummingbirds

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ABSTRACT

Fat deposition and torpor use in hummingbirds exhibiting distinct foraging styles should vary. We predicted that dominant territorial hummingbirds will use torpor less than subordinate nonterritorial species because unrestricted access to energy by territory owners allows for fat storage. Entry into torpor was monitored using open-flow respirometry on hummingbirds allowed to accumulate fat normally during the day. Fat accumulation was measured by solvent fat extraction. Territorial blue-throated hummingbirds (*Lampornis clemenciae*) had the highest fat accumulation and used torpor only 17% of the time. Fat storage by *L. clemenciae* averaged 26% of lean dry mass (LDM) in 1995 and 18% in 1996, similar to that measured for other nonmigratory birds. Fat storage by magnificent hummingbirds (*Eugenes fulgens*; trapliner) and black-chinned hummingbirds (*Archilochus alexandri*; nectar robber) averaged 19% and 16% of LDM, respectively, and they used torpor frequently (64% and 92% of the time, respectively). All species initiated torpor if total body fat dropped below 10% of LDM, indicating the existence of a torpor threshold. The ability of *L. clemenciae* to store enough fat to support nighttime metabolism is likely an important benefit of territoriality. Likewise, frequent torpor use by subordinates suggests that natural restrictions to energy intake can impact their energy budget, necessitating energy conservation by use of torpor.

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Introduction

Hummingbirds are truly species that test the limits of endothermic physiology. Their extremely small size results in metabolic demands that are among the highest recorded (Powers and Nagy 1988; Weathers and Stiles 1989; Powers and Conley 1994). High metabolic rates likely make it difficult for hummingbirds to store energy (King 1972; Hainsworth 1978). In fact, the allometric prediction of daytime fat storage for a 3–5-g hummingbird is only 0.2 g (Calder 1974, eq. [46]), roughly equivalent to the amount needed to meet their nighttime metabolic demands if they remained normothermic. It is clear that efficient management of energy reserves by hummingbirds is crucial to their survival.

A hummingbird's most important safeguard against negative energy balance is their ability to use torpor. When hummingbirds enter torpor, metabolic rate decreases and body temperature (T_b) drops as much as 20°–30°C. Use of torpor results in a substantial energy savings by lowering nighttime energy expenditures (Lasiewski 1963; Krüger et al. 1982; Hiebert 1990). However, the use of torpor by hummingbirds may have potential costs. When hummingbirds enter torpor, they become virtually helpless, and it has been suggested that they are most susceptible to predation during this time (Hainsworth et al. 1977). It is also possible that use of torpor slows down incubation (Calder and Booser 1973), interferes with sleep patterns (Hiebert 1990), and possibly prolongs molt (Hiebert 1992, 1993). These potential costs suggest strongly that hummingbirds should minimize the amount of time spent in torpor.

Several studies during the past 40 years have attempted to clarify patterns of torpor use in hummingbirds (e.g., Lasiewski 1963; Wolf and Hainsworth 1972; Krüger et al. 1982; Bech et al. 1997). However, data from these studies are variable and difficult to interpret because energy budgets were not considered. Recent studies have attempted to rectify this problem by simultaneously tracking changes in body mass with patterns of torpor use (Carpenter and Hixon 1988; Hiebert 1990, 1991, 1992). One of the more important contributions of these studies is the observation that the functional significance of torpor is not confined to immediate energy crises, as suggested by Hainsworth et al. (1977), but may also play a role in maximizing the rate of energy storage in preparation for migration and molt (Carpenter and Hixon 1988; Hiebert 1993). While these studies provide key insights into the functionality of torpor for

hummingbirds, they still do not address questions related to the role torpor plays in balancing a daily energy budget.

In a key study by Hiebert (1992), molting rufous hummingbirds (*Selasphorus rufus*) were shown to initiate torpor only after energy reserves (presumably fat) fell below some critical threshold level. In this study the threshold decreased throughout the night to minimize the chance of initiating torpor, presumably because torpor use would slow down growth of new feathers. This was the first study to convincingly link energy management on a daily basis to torpor regulation. It follows, then, that any factor causing energy stores to drop below a critical threshold should result in torpor initiation. This is supported by the fact that captive birds increase torpor use when food is restricted (Hiebert 1991; Bech et al. 1997). It is likely that when food is restricted for free-living birds, torpor will be used more frequently as well. In natural hummingbird communities it is common to have dominant territorial individuals or species that restrict access of subordinates to food (Ewald and Carpenter 1978; Pimm et al. 1985; Feinsinger 1986; Ewald and Bransfield 1987; Sandlin 2000b). Thus, we would hypothesize that subordinate species should use torpor more frequently than dominant species. If this hypothesis is correct, and use of torpor does have the negative consequences described above, then the ability of dominant species to avoid torpor would be advantageous in these competitive relationships.

In this study we tested the hypothesis that subordinate species use torpor more frequently than dominant species in a natural hummingbird assemblage in southeastern Arizona. The assemblage consists of one dominant and two subordinate species, which have been well studied with regard to their social interactions (Pimm 1978; Pimm et al. 1985; Powers and Conley 1994; Powers and McKee 1994; Sandlin 2000a, 2000b). The blue-throated hummingbird (*Lampornis clemenciae*; ca. 8.0 g) is the largest North American hummingbird and successfully excludes other hummingbirds from high-quality food resources (Pimm et al. 1985; Powers and Conley 1994; Powers and McKee 1994; Sandlin 2000b). Because of their dominance over other hummingbirds, *L. clemenciae* has a relatively high foraging efficiency because they are often able to feed alone and unbothered by other birds (Sandlin 2000b). Easy access to their food source should make it possible for *L. clemenciae* to store sufficient energy to support their nocturnal fast. Thus, we hypothesize that *L. clemenciae* should use torpor infrequently. The black-chinned hummingbird (*Archilochus alexandri*; ca. 3.0 g) is a classical subordinate species that makes a living by robbing nectar from *L. clemenciae* territories or by foraging in suboptimal habitat (Pimm et al. 1985; Powers and Conley 1994; Powers and McKee 1994; Sandlin 2000b). Because their access to food is restricted by *L. clemenciae*, making energy storage more difficult, we hypothesize that *A. alexandri* should use torpor more frequently than *L. clemenciae*. A second subordinate species is the magnificent hummingbird (*Eugenes fulgens*;

ca. 7.5 g). Although subordinate to *L. clemenciae* (Pimm et al. 1985; Sandlin 2000b), *E. fulgens* does not appear to frequently engage in agonistic interactions (Sandlin 2000b; D. R. Powers, personal observation). *Eugenes fulgens* seems to avoid competition with *L. clemenciae* by foraging as a trapliner where they travel a regular circuit between widely spaced nectar sources (Powers 1996). In addition, they may also switch, at least in part, from nectarivory to arthropod foraging (J. A. Van Hook, D. R. Powers, E. A. Sandlin, and T. J. McWhorter, unpublished data). Even though *E. fulgens* appears to avoid substantial competition with *L. clemenciae*, we suspect that their foraging method is not as efficient as territoriality and hypothesize that they will still need to use torpor more frequently than *L. clemenciae*.

While it is difficult to measure torpor use in free-living hummingbirds, in this study we attempted to evaluate the importance of torpor to birds utilizing different foraging strategies, and whose energy stores were gained under natural conditions. Frequency of torpor use was determined in the laboratory for birds collected at dusk, just before the nocturnal fast, by measuring nighttime metabolic rate at ambient temperatures (T_a) similar to what they normally experience in the wild. Thus, birds were not forced to use torpor because of unnatural thermoregulatory stress. We measured total body fat in each of the species to determine whether energy storage patterns differed between species using the different foraging methods and whether energy storage pattern was related to frequency of torpor use. Should it be shown that the subordinate species use torpor more frequently than *L. clemenciae*, then insight will be gained not only into how energy stores impact torpor use but also into what it means to be a dominant versus subordinate individual in a hummingbird social system.

Material and Methods

Study Site and Animals

We conducted this study in the Chiricahua Mountains (Cochise County) of southeastern Arizona (latitude 31°50′N, longitude 109°15′W; 1,700 m altitude) during June and July of 1995 and 1996. During this time of year, seasonal and physical factors that influence torpor use (e.g., temperature, molt, and migration; Hiebert 1993) are minimized, increasing the likelihood that competitive ability is a major factor in energy storage.

The area surrounding the study site is characterized by riparian habitat bordered by oak woodland and a mixed coniferous/deciduous forest and is the preferred habitat of the species used in this study. A more detailed description of the habitat can be found in Pimm et al. (1985).

Three hummingbird species common to this area were used in this study: the dominant blue-throated hummingbird (*Lampornis clemenciae*), whose North American range extends only into the southeastern portions of Arizona, southwestern New Mexico, and parts of southern Texas (Williamson 2000); the

traplining magnificent hummingbird (*Eugenes fulgens*), whose range, although more expansive than that of *L. clemenciae*, is still restricted to the southern portions of the southwestern United States (Powers 1996); and the subordinate black-chinned hummingbird (*Archilochus alexandri*), which can be found in most regions of the western United States (Baltosser and Russell 2000).

Metabolic Trials

For the purpose of this experiment we assumed that a bird entered torpor when metabolic rate (oxygen consumption) abruptly fell below rest-phase normothermic levels (Hiebert 1990). We measured O_2 consumption ($\dot{V}o_2$) with an open-circuit, positive pressure respirometry system. Body mass was measured before and after the respirometry trials with a top-loading electronic balance accurate to 0.01 g (Metler BB240). Measurements were made continuously throughout the night on birds held in a metabolism chamber under the T_a conditions and photoperiods described below. Initially, birds were allowed to feed on 25% (0.73 M) sucrose solution ad lib. in order to fill their crop just before beginning a metabolic trial. Previous studies suggest that hummingbirds will fill their crops before roosting to store energy for the nocturnal fast (see Powers 1991 for discussion).

Metabolism chambers were constructed from canning jars with an effective volume of 380 mL for *A. alexandri* and 800 mL for *L. clemenciae* and *E. fulgens*. T_a inside the chamber was monitored with a Cu-Cn thermocouple and recorded to the nearest 0.1°C with a Physiotemp Bat-12. Thermocouples were calibrated against thermometers traceable to the National Bureau of Standards.

We regulated the flow of dry, CO_2-free air through the metabolism chamber at 500 mL/min (STPD). Flow rate was regulated by a Cole-Parmer rotameter (previously calibrated with a bubble meter; Levy 1964) upstream from the chamber. Barometric pressure and T_a were recorded in order to correct flow to STPD. A sample of outlet air was passed through soda lime and Drierite to remove CO_2 and water vapor, respectively, before going through an Ametek (now Applied Electrochemistry) S-3A O_2 analyzer. We used $\dot{V}o_2$ as an indirect measure of metabolic rate. Before each $\dot{V}o_2$ run we calibrated the O_2 analyzer with dry, CO_2-free room air, assuming an O_2 concentration of 20.95%. Data were recorded and analyzed using an Apple Power Macintosh 7200 computer running Warthog Lab Helper and Lab Analyst software (courtesy of Mark Chappell). Output from the analyzer was recorded every 10 s, with baseline values being recorded at the beginning and end of each hour.

Birds were captured, placed in a metabolism chamber, and housed for the duration of the experiment in a Percival I-35L environmental chamber set at 25°C. Metabolic rate was measured for 0.5 h beginning at the top of each hour, with baselines measured at the beginning and end of the run. When the run was complete, T_a was lowered 2°C to the next experimental T_a. T_a reductions of 2°C/h were continued throughout the night. This rate of T_a reduction closely approximates the nighttime T_a experienced by free-living birds (D. R. Powers, unpublished data). We simulated natural cycles of T_a in an effort to make our laboratory data relevant to wild birds in their natural habitat. Metabolic measurements were terminated when a bird entered torpor or at the conclusion of the nighttime period if a bird remained normothermic. At this point, birds were killed for measurement of total body fat.

Total Body Fat

We measured daytime fat accumulation by doing whole-body fat extractions on birds captured at dusk before their nocturnal fast (control group; $n = 6$ per year for each species). Fat was extracted from birds used in the metabolic trials to determine body-fat content of birds at the conclusion of the nocturnal fast or upon entry into torpor (experimental group). Fat use during the nocturnal fast was estimated by subtracting the fat content of experimental birds from the average value of the control birds.

To extract total body fat, birds were killed and dried to a constant mass in an oven at 60°C. The difference between the initial wet mass (WM) and the final dry mass (DM) was considered the bird's total body water. To measure lean dry mass (LDM), the dried body was cut into tiny pieces, placed into a 25 mm × 80 mm extraction thimble (Schleicher & Schuell), placed back into the oven for 1 h, and then weighed (both thimble and tissue together) to the nearest 0.001 g on a Metler College B303 balance. The above weighing procedure was repeated until the thimble plus tissue maintained a constant mass over three consecutive measurements. After weighing, the thimble was placed into a Soxhlet extraction apparatus (125-mL flask capacity; Ace Glass) containing an ether solvent. Extractions were run for approximately 24 h, after which the thimble and its contents were removed from the Soxhlet and air dried. After air drying, the thimble and contents were placed in the 60°C oven and dried to a constant mass as described above. The difference between the DM and LDM was considered the fat mass (FM) of the bird.

Statistical Analysis

Because our study species differed in mass, we evaluated the impact of body mass on our data using ANCOVA with body mass as the covariate. It is important to do this because body-fat data are reported as ratios for the sake of comparison, and such ratios can be misleading under certain circumstances. For example, if fat storage rate were a function of body size, then reporting data in this manner would be inappropriate (Blem 1980).

Between-year differences in means for a single species were

tested using a standard Student t-test. Measurements involving more than two groups were tested using ANOVA (with Tukey test for post hoc analysis), or χ^2 goodness of fit when assumptions for parametric analysis of more than two groups could not be met. Homogeneity of variance between sample groups was determined using a Levene's test for homogeneity. Seasonal and interspecific differences in torpor use were tested using contingency tables and χ^2 analysis.

Results

Lampornis clemenciae used torpor less frequently than *Archilochus alexandri* and *Eugenes fulgens* in both 1995 and 1996 (Fig. 1). Between-year differences in torpor use for all three species were not significantly different. If data from both years are combined, frequency of torpor use is 17% (two of 12) for *L. clemenciae*, 92% (12 of 13) for *A. alexandri*, and 64% (seven of 11) for *E. fulgens*.

Nighttime metabolic profiles and times of entry into torpor for individuals of all three species are shown in Figure 2. Metabolic profiles differed between years and are shown separately. For *L. clemenciae*, mean $\dot{V}o_2$ as a function of T_a was the same in both years, but the variation in $\dot{V}o_2$ was significantly higher in 1996 ($F_{1,90} = 13.67$, $P < 0.001$). In both years mean $\dot{V}o_2$ was higher than predicted at all T_a's (Lasiewski and Lasiewski 1967). Higher than predicted $\dot{V}o_2$ occurring in all species might, at least in part, be due to specific dynamic action resulting from digestion of crop contents. For *A. alexandri*, nighttime $\dot{V}o_2$ was significantly higher in 1995 than in 1996 ($F_{1,5} = 6.10$, $P < 0.001$), while interindividual variation did not change ($F_{1,60} = 0.866$, $P = 0.356$). In 1995 $\dot{V}o_2$ was higher than predicted while in 1996 $\dot{V}o_2$ was similar to predicted values (Lasiewski 1963). It must be noted that because *A. alexandri* used torpor frequently, these metabolic profiles are based on relatively few measurements. Thus, the observed differences need to be interpreted cautiously. Metabolic profiles for *E. fulgens*

differed markedly between years. In 1995 only one individual remained normothermic beyond midnight. The $\dot{V}o_2$ of this individual was consistently higher than predicted (Lasiewski and Lasiewski 1967). In 1996 individuals initiated torpor later and had a more variable $\dot{V}o_2$. No meaningful statistical comparison of $\dot{V}o_2$ measurements could be made for *E. fulgens* because data were too few in the latter portion of the measurement period.

ANCOVA showed that neither WM ($F_{1,46} = 0.315$, $P = 0.578$) or LDM ($F_{1,46} = 0.863$, $P = 0.358$) contributed significantly to the values of FM measured in this study. Thus, we did not correct for the effects of body mass in the analyses below.

Fat storage differed between years only for *L. clemenciae* (Fig. 3; $F_{1,16} = 8.64$, $P = 0.01$), where FM in control birds was on average 27% lower in 1996. This was also the only year *L. clemenciae* was observed to initiate torpor (Fig. 1). LDM of *L. clemenciae* did not differ between years ($t_8 = 0.37$, $P = 0.723$). In both years, experimental values of FM were significantly lower than control values (Fig. 3; $F_{1,16} = 17.87$, $P = 0.001$), indicating that fat catabolism contributed to nighttime energy expenditure. Total daytime fat accumulation in both years was 0.23 g/d (8.9 kJ/d). Data for *A. alexandri* and *E. fulgens* did not differ significantly between years, so 1995 and 1996 measurements have been combined for analysis (Fig. 4). Because only one control measurement was made for *E. fulgens* in 1995, we have combined it with the 1996 control data for analysis. In both species control data differed significantly from the experimental (Fig. 4; *A. alexandri*, $t_{18} = 2.65$, $P = 0.016$; *E. fulgens*, $t_{12} = 2.41$, $P = 0.033$), indicating that fat catabolism contributed to nighttime energy expenditure. Total daytime fat accumulation was 0.18 g/d (7.0 kJ/d) for *E. fulgens* and 0.03 g/d (1.2 kJ/d) for *A. alexandri*. These values are 78% and 13% of that observed for *L. clemenciae*, respectively.

Daytime proportional fat mass (control) in *L. clemenciae* averaged about 26% of LDM (8% of WM) in 1995 and 18% of LDM (6% of WM) in 1996. During 1995, *L. clemenciae* had a higher proportional fat mass during the day than *A. alexandri* (16% LDM, 5% WM) or *E. fulgens* (19% LDM, 6% WM; $\chi^2_2 = 8.62$, $P = 0.013$), but in 1996, daytime proportional fat mass was not statistically distinguishable between species ($\chi^2_2 = 0.73$, $P = 0.695$). Proportional fat mass at the conclusion of the torpor trials (experimental) did not vary among species in either year (1995, $\chi^2_2 = 2.02$, $P = 0.364$; 1996, $\chi^2_2 = 2.35$, $P = 0.309$), so experimental birds are lumped for analysis. When proportional fat mass for all experimental birds are plotted as a function of time, the slope of the resulting relationship is indistinguishable from 0 regardless of whether LDM or WM is used as the dependent variable (Fig. 5). This suggests a constant torpor threshold similar to model 1 in Hiebert (1992). The mean FM value for this threshold is 10.35% ± 3.5% ($n = 29$) of LDM and 3.97% ± 1.34% for WM ($n = 29$).
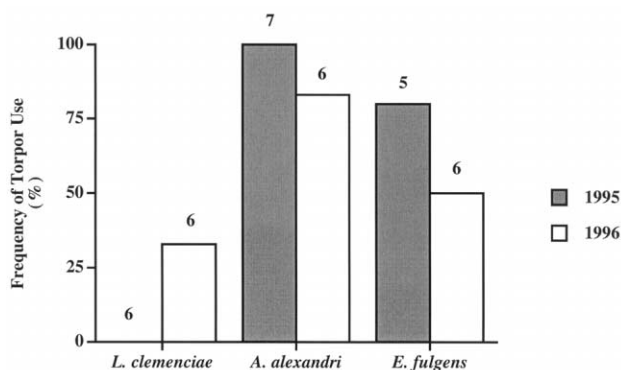

Figure 1. Proportion of *Lampornis clemenciae*, *Archilochus alexandri*, and *Eugenes fulgens* that entered torpor during experimental trials in 1995 and 1996. Numbers above bars are sample sizes.
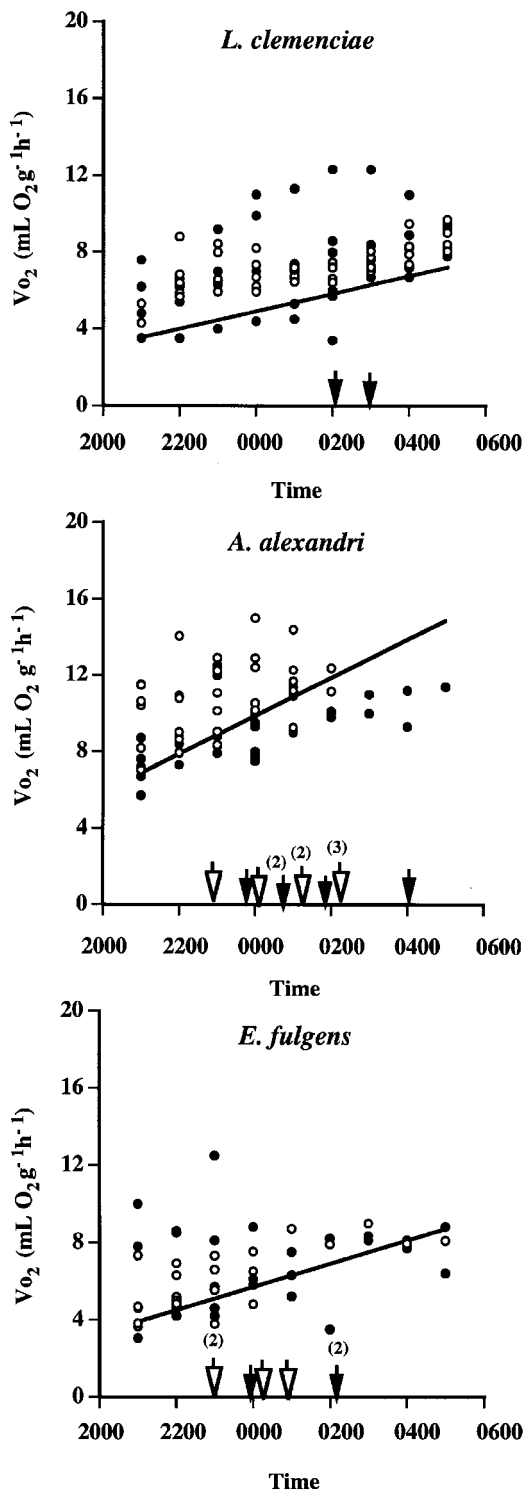
Figure 2. Hourly metabolic rate for *Lampornis clemenciae*, *Archilochus alexandri*, and *Eugenes fulgens* during metabolic trials in 1995 (*open circles*) and 1996 (*solid circles*). The line represents the predicted relationship between metabolic rate and temperature (Lasiewski and Lasiewski 1967 for *L. clemenciae* and *E. fulgens*; Lasiewski 1963 for
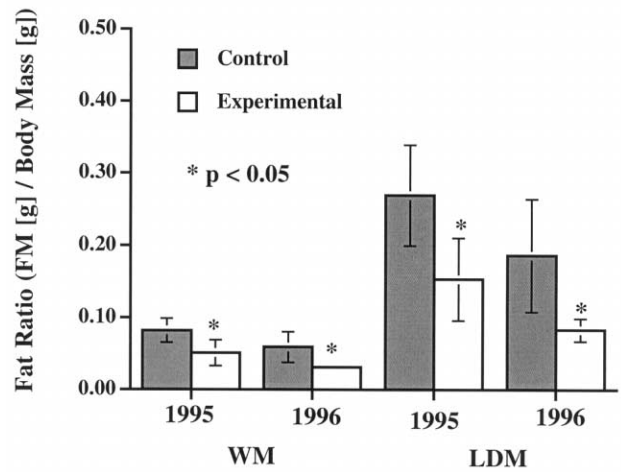

Figure 3. The ratio of total body fat to wet mass (*WM*) and lean dry mass (*LDM*) in *Lampornis clemenciae* during 1995 and 1996. Data are presented as mean ± SD.

Discussion

In this study *Lampornis clemenciae* was the only species not to use torpor with some regularity (Figs. 1, 2). *Lampornis clemenciae* is the dominant species in the system (Pimm et al. 1985; Powers and Conley 1994; Sandlin 2000*b*) and the only species with unrestricted access to their energy source. This free access to food allowed them to store fat during the day that was in excess of 26% of LDM (8% of WM) in 1995. While fat storage by *L. clemenciae* was proportionally higher than that of the other species in this study, it was substantially less than that found in male ruby-throated hummingbirds (*Archilochus colubris*; ca. 3.0 g) during late summer and fall (Norris et al. 1957). The discrepancy between FM in *L. clemenciae* and *A. colubris* probably reflects premigratory fattening in the latter study, which may be associated with the deposition of fat stores equivalent to >40% of LDM (Baggott 1986; Carpenter and Hixon 1988; Gudmundsson et al. 1991; Kaiser 1992; Hiebert 1993). On the other hand, the difference in FM of *L. clemenciae* between 1995 and 1996 may be related to differences in the sucrose solutions we provided (1 M in 1995 vs. 0.5 M in 1996). The ability of hummingbirds to assimilate energy is constrained by the amount of water in nectar (McWhorter and Martínez del Rio 1999), and the interannual difference in FM likely reflects this constraint. This argument is strengthened by the observation that the reduction in feeder energy content is similar to the observed reduction in FM.

In contrast, *Archilochus alexandri* relied on regular torpor to

A. alexandri). The predicted increase in metabolic rate is based on our simulated nighttime temperature cycles. Arrows (*open* = 1995, *solid* = 1996) represent times when individual birds entered torpor.
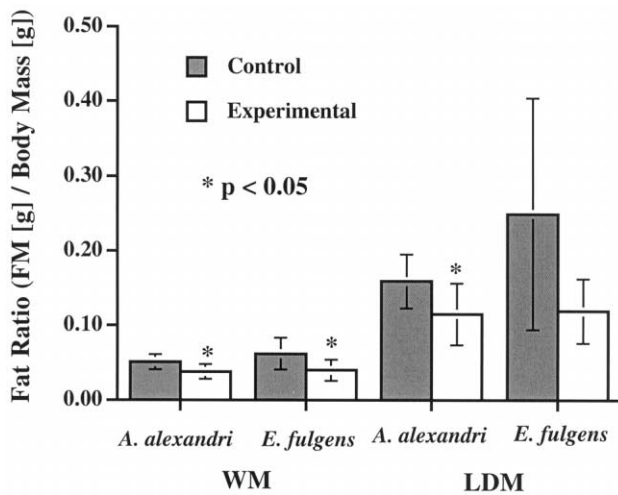
Figure 4. The ratio of total body fat to wet mass (*WM*) and lean dry mass (*LDM*) in *Archilochus alexandri* and *Eugenes fulgens*. Bars represent combined data from 1995 and 1996.

balance their energy budget (Figs. 1, 2). Unlike *L. clemenciae*, only a small amount of body fat was catabolized before torpor initiation (Table 1; Fig. 4). On average, torpor was initiated when total body fat reached about 10% of LDM (4% of WM), suggesting that this level of fat storage is a threshold. In fact, this threshold seemed to be applicable for all species in this study (Fig. 5). For birds that remained normothermic, proportional fat mass was about 10% of LDM at the end of the nocturnal fast. These data are consistent with the notion of an energy-storage threshold for torpor initiation proposed by Hiebert (1992). Our data differ from those of *Selasphorus rufus* reported by Hiebert in that the threshold for our birds is not time dependent. Rather, the threshold appears constant throughout the night, conforming to Hiebert's (1992) model 1. This difference in threshold management might be due to the fact that birds in our study did not have the concern of delaying molt, as was the case with *S. rufus*. It should be noted that we have few measurements between 4:00 and 5:00 A.M. The two values we do have during this period are lower, so it is possible that more data during this interval could show a time-related change in the torpor threshold.

The fat-storage threshold for torpor initiation in hummingbirds supports the existence of a cellular signaling mechanism that senses changes in body lipid content and initiates compensatory physiological changes when lipid levels fall below threshold. The idea of a "lipostat" has been proposed for mammals and supported by evidence that the peptide hormone leptin, secreted primarily by white adipose tissue, might be involved in the regulation of fat mass in hibernating mammals (Boyer and Barnes 1999). It is possible that leptin receptors are a component of this proposed lipostat. Whether or not such

mechanisms function in birds is unclear and will require further studies.

Eugenes fulgens did use torpor but less frequently than *A. alexandri* (Figs. 1, 4). Even though *E. fulgens* was subordinate to *L. clemenciae*, they rarely engaged in direct competitive interactions (Sandlin 2000*b*). This is likely because *E. fulgens* foraged as a trapliner (Powers 1996) and seemed to be able to substitute arthropods for nectar as an energy source rather than compete directly with *L. clemenciae* (J. A. Van Hook, D. R. Powers, E. A. Sandlin, and T. J. McWhorter, unpublished data). Because *E. fulgens* acquires a substantial portion of their energy outside of areas defended by *L. clemenciae*, the high variability in torpor use might reflect variability in an individual's ability to locate sufficient alternative energy resources or perhaps daily variation in the availability or quality of alternative resources.

If we assume that hummingbirds avoid torpor whenever possible, then frequency of torpor use can be used to address questions about the energetic advantage of various foraging strategies. Several studies have shown that territory defense by nectar-feeding birds is related to energy density within the defended area (see, e.g., Gill and Wolf 1975; Gass et al. 1976; Kodric-Brown and Brown 1978) and that territoriality is abandoned when the energy value of the territory falls below that required to sustain the territory owner (Gill and Wolf 1975; Kodric-Brown and Brown 1978). Likewise, several studies have clearly shown that the foraging dynamics of this hummingbird
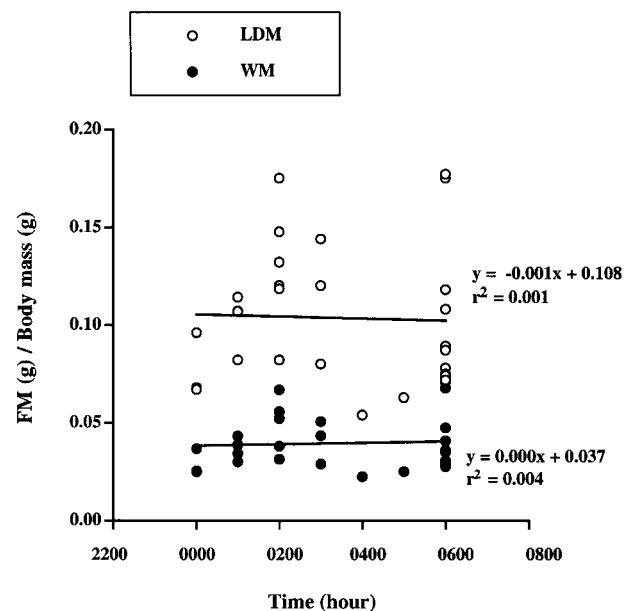

Figure 5. Ratio of total body fat to lean dry mass (*LDM*) and wet mass (*WM*) for all species at the time of entry into torpor or at the conclusion of the nocturnal fast if they remained normothermic. The slope of the regression lines is not significantly different from 0, indicating that the birds will not allow their total body fat to fall below this minimum level (torpor threshold).

Table 1: Mean ± SD of total body (wet) mass (WM), lean dry mass (LDM), and fat mass (FM) for each of the study species

Species	Control				Experimental			
	n	WM (g)	LDM (g)	FM (g)	n	WM (g)	LDM (g)	FM (g)
Lampornis clemenciae:								
1995	5	7.99 ± .11	2.46 ± .22	.65 ± .14	5	8.16 ± .19	2.76 ± .07	.42 ± .15
1996	5	8.15 ± .19	2.74 ± .61	.48 ± .16	5	8.06 ± .45	3.01 ± .28	.25 ± .05
Archilochus alexandri	10	2.97 ± .21	.96 ± .10	.15 ± .03	10	3.06 ± .29	1.06 ± .26	.12 ± .03
Eugenes fulgens	7	8.00 ± .48	2.52 ± 1.21	.49 ± .16	9	7.59 ± .42	2.59 ± .29	.31 ± .11

Note. Because values for *L. clemenciae* differed between years, 1995 and 1996 data are presented separately.

guild are energy dependent (Pimm et al. 1985; Powers and Conley 1994; Powers and McKee 1994; Sandlin 2000*b*). In this study, *L. clemenciae* was the only species to consistently exhibit positive energy influx adequate to support nighttime normothermy. This suggests that territorial foraging by *L. clemenciae* resulted in a higher net energy gain than for either *A. alexandri* or *E. fulgens* (Gill 1978), particularly in 1995. This advantage to territorial *L. clemenciae* males is potentially enormous assuming the risks associated with torpor use, and the danger of starvation is truly minimized, as suggested by our laboratory results. Thus, the amount of energy required to sustain a successful territorial male *L. clemenciae* might also include that needed to accommodate daytime fat accumulation and normothermic nighttime metabolism. This idea is indirectly supported by Powers and Conley (1994), who measured field metabolic rate (FMR) in *L. clemenciae* and *A. alexandri* using doubly labeled water. They showed that FMRs of these species were 87% and 17% higher than predicted, respectively. Even though relative FMR was substantially higher in *L. clemenciae* (likely due to agonistic behavior), they generally gained body mass during the measurement period, whereas *A. alexandri* generally lost body mass. This indicates a commitment to energy storage in spite of the high energy demands of territoriality.

While the subordinate species seemed to remain in energy balance, they engaged in less fat deposition (Table 1; Fig. 4). It is unclear whether the lower levels of fat storage were due to reduced energy intake or higher foraging costs (or both?). Colwell (1973) suggested that when food resources are highly predictable and in good supply that opportunistic feeders can meet their energy needs. The feeders defended by *L. clemenciae* certainly fit this criterion. The ideas of Colwell are supported by the fact that when nectar availability is essentially unlimited, *A. alexandri* are excluded from *L. clemenciae* territories much less frequently than when nectar availability is restricted (Powers and Conley 1994). It is also possible that the subordinate species are more actively managing their energy budgets to assure energy balance. Tiebout (1991) suggested that when energy availability to the trapline foraging *Chlorostilbon canivetii* was constrained that they increased the energy available for flight (to forage) by reducing perch-related activities such as

preening, calling, and "wing buzzing" (beating their wings while remaining perched). It is unclear if subordinate species in this study make such metabolic adjustments, but birds do exhibit behaviors that are presumably designed to minimize the number of agonistic encounters with *L. clemenciae*. *Archilochus alexandri*, for example, will perch out of sight of an *L. clemenciae* male and feed only after the male has left on a chase (D. Powers, personal observation). When *A. alexandri* get such an opportunity, their feeding bout will last longer than is typical for the territory owner (Tiebout 1993; Sandlin 2000*b*; D. Powers, personal observation).

Active management of energy budgets by the subordinate species does not eliminate the energetic asymmetry that exists with the territorial *L. clemenciae*. Both *A. alexandri* and *E. fulgens* required frequent use of torpor to prevent energy stores from falling below acceptable levels. The energetic asymmetry was probably greatest between *L. clemenciae* and *A. alexandri* since *A. alexandri* need to use torpor nearly 100% of the time. The metabolic demands of their small size coupled with their reliance on an energy resource controlled by *L. clemenciae* probably made it extremely difficult for *A. alexandri* to balance their energy budget without using torpor. The relative contribution of body size and competition to the torpor use pattern exhibited by *A. alexandri* is unclear. However, differences in torpor use by *L. clemenciae* and *E. fulgens*, which are similar in size, suggest that restricted energy availability to a subordinate species can alter the frequency with which torpor is employed.

It is important to note that the patterns of torpor use reported in this study might have been impacted by stresses associated with laboratory measurements. Geiser et al. (2000) suggest that torpor bouts by daily heterotherms in the field are often longer and deeper (i.e., achieve a lower T_b) than in the laboratory. Extended periods of captivity can lead to physiological and behavioral changes that make animals different from free-living individuals. Carlstead (1996) suggests that this is at least in part due to a captive animal's inability to alter external stimulations (e.g., behavioral thermoregulation, initiation of foraging in response to hunger, etc.). The resulting behavioral and physiological changes that occur due to captivity are dif-

ficult to predict because they can vary between species (Geiser et al. 2000; Navas and Gomes 2001).

Even though conditioning effects of extended captivity were omitted from this study, stress resulting from capture and handling undoubtedly occurred (Wingfield and Ramenofsky 1999). Capture and handling stress is unavoidable in this type of study, and its effects are not reliably predictable (Cockrem and Silverin 2002; Romero and Romero 2002). Thus, potential stress effects should be kept in mind as these data are applied to future field studies.

In this study we have gained several insights into how free-living hummingbirds manage torpor use. We have shown that *L. clemenciae* was able to store more fat and use torpor less frequently than either *E. fulgens* or *A. alexandri*. This supports our hypothesis that unrestricted access to food by a territorial species will allow them to more regularly support normothermy during their nocturnal fast. Limiting torpor use might be advantageous to *L. clemenciae* because the associated consequences are avoided. Likewise, our hypothesis that *E. fulgenes* and *A. alexandri*, subordinate species, would use torpor more frequently because their access to food (energy) was restricted by *L. clemenciae* was also supported. Balancing their energy budget was particularly difficult for *A. alexandri* because of the high energy demands associated with their small body size. This is evidenced by *A. alexandri*'s inability to store fat and their use of torpor almost every night. We have also shown that food quality might impact torpor use, particularly in *L. clemenciae*, who only used torpor in 1996, when the energy content of their feeder solution was cut in half. Lower energy intake, resulting in lower fat storage, might be evidence for a foraging constraint (e.g., water elimination rate). The highly variable rate of torpor use exhibited by *E. fulgens* might also be the result of variability in food sources utilized during trapline foraging. Finally, our data suggest that torpor in all three species is initiated at night when total body fat falls below a threshold level (about 10% of LDM) and that the threshold remains constant throughout the nocturnal fast.

Acknowledgments

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