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ARTHROPOD FORAGING BY A SOUTHEASTERN ARIZONA HUMMINGBIRD GUILD

DONALD R. POWERS,[1,4] JESSAMYN A. VAN HOOK,[1]
ELIZABETH A. SANDLIN,[2] AND TODD J. McWHORTER[2,3]

ABSTRACT.—We tested the hypothesis that foraging for arthropods may be a viable source of energy when hummingbirds are competitively excluded from sources of nectar. We hypothesized that the Magnificent Hummingbird (*Eugenes fulgens*) relies more upon arthropods than the Blue-throated Hummingbird (*Lampornis clemenciae*) or Black-chinned Hummingbird (*Archilochus alexandri*) in southeastern Arizona. We were unable to quantify arthropod foraging by *A. alexandri*, but measured frequent arthropod foraging by both *E. fulgens* and *L. clemenciae*. *E. fulgens* engaged in more aerial flycatching than *L. clemenciae*, and their rate of flycatching attempts was higher than by *L. clemenciae*. Analysis of gut contents showed that *E. fulgens* consumes the greatest diversity of arthropods. Respiratory quotient measurements indicated *E. fulgens* catabolized a greater amount of fat/protein than the other species. Gut morphology of *E. fulgens* does not appear to differ from other hummingbirds suggesting hummingbirds in general may have the ability to use arthropods as an alternative energy source when access to floral energy is restricted. Our data are consistent with the hypothesis that the diet of *E. fulgens* includes more arthropods than other species with which they compete. *Received 10 November 2009. Accepted 3 February 2010.*

Floral nectar has been assumed to be the primary energy resource of hummingbirds. This is reasonable from both ecological and physiological perspectives when one considers that many aspects of hummingbird and floral natural history are intertwined (Feinsinger 1983, Stiles 1995), and that sugars in floral nectar are quickly and easily digested. It is also known that hummingbirds supplement their diets with small arthropods as floral nectar lacks many important nutrients (Baker 1977). However, arthropods are generally considered to be of little energetic importance for hummingbirds (Wolf and Hainsworth 1971).

Hummingbirds often spend <10% of their day foraging for arthropods when nectar is in sufficient supply (Gass and Montgomerie 1981). There is evidence that arthropod consumption increases during specific periods of the natural cycle of hummingbirds such as during reproduction, specifically by nesting females (Murphy 1996), and during periods of low nectar availability (Chavez-Ramirez and Dowd 1992). Time spent on other activities, including nectar foraging, is likely reduced when time spent foraging for arthropods increases (Chavez-Ramirez and Dowd 1992). Stiles (1995) argued that hummingbirds acquire a meaningful amount of energy from consumption of arthropods, which would be needed to meet energy demands when nectar intake is reduced. This is not difficult to imagine since arthropods have high energy content (Weathers and Sullivan 1989) and appear to be fully digested in a hummingbird's digestive tract (Remsen et al. 1986).

We know of no studies that examined the possibility that hummingbirds might use arthropods when excluded from a nectar source because of local social interactions. For example, an aggressive dominant species could restrict access of subordinate species to clumps of flowers contained within its territory forcing the subordinate species to seek alternative energy sources (Young 1971). This may reduce the energetic impact of competition if the subordinate could use arthropods as a primary energy source. This attribute would provide ecological separation between competitors so they can coexist (Rosenzweig 1985, Sandlin 2000b) in areas that do not provide abundant nectar resources (Brown et al. 1978).

Eugenes fulgens (Magnificent Hummingbird) is a member of a three-species hummingbird guild seasonally inhabiting the Chiricahua Mountains of southeastern Arizona. *E. fulgens* will readily feed on nectar in artificial feeders, but use declines when feeders are defended by dominant Blue-throated Hummingbirds (*Lampornis clemenciae*) (Pimm et al. 1985, Powers and Conley 1994, Sandlin 2000a, Powers et al. 2003). This behavior is substantially different from that exhibited by

[1] Biology Department, George Fox University, 414 North Meridian Street, Newberg, OR 97132, USA.
[2] Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA.
[3] School of Animal and Veterinary Sciences, University of Adelaide, Roseworthy Campus, SA 5371, Australia.
[4] Corresponding author; e-mail: dpowers@georgefox.edu

Black-chinned Hummingbirds (*Archilochus alexandri*), another subordinate species, which consistently intrudes on *L. clemenciae* territories in attempts to gain a nectar reward (Powers and Conley 1994). There are few natural flowers available in many portions of the Chiricahua Mountains prior to onset of monsoon rains, and arthropods may be the only nearby alternative energy source for *E. fulgens* (Pimm et al. 1985). The idea that *E. fulgens* has the ability to subsist only on arthropods is not new. Marshall (1957:81) suggested that *E. fulgens* can inhabit pine-oak (*Pinus* spp.–*Quercus* spp.) woodlands because it ''can dispense with moist habitat and flowers'' and switch to arthropod consumption.

We conducted this study to ascertain if arthropods could be used as an alternative energy source when nectar availability is restricted and if the use of arthropods for energy is a feasible strategy that allows *E. fulgens* to reduce competitive interactions with territorial *L. clemenciae*. Evidence from behavioral, morphological, and physiological experiments are presented to demonstrate the energetic importance of arthropod foraging to hummingbirds.

METHODS

Study Animals.—Males of three species were used in this study: *E. fulgens* (~7.5 g), *L. clemenciae* (~8.0 g), and *A. alexandri* (~3.0 g). All three species occur in southeastern Arizona during summer and use different foraging strategies (Pimm et al. 1985, Powers and Conley 1994, Sandlin 2000a). *L. clemenciae* is a dominant species, defending territories along borders of riparian canyons. *A. alexandri* is non-territorial at our study site and robs nectar from territories defended by *L. clemenciae*. *E. fulgens* is also non-territorial, but appears to forage as a trapliner (Powers 1996), avoiding many competitive interactions at dense flower aggregations.

Study Area.—This study was conducted at the American Museum of Natural History's Southwestern Research Station in the Chiricahua Mountains, Cochise County, Arizona (31° 50′ N, 109° 15′ W; 1,700 m asl). Habitat at the station is largely riparian, bordered by oak woodland and a mixed deciduous/coniferous forest. Pimm et al. (1985) provide a more detailed description of the habitat. This forest endures a pronounced dry season from November until monsoon rains begin in early July that can dramatically affect the amount of nectar available (Li and Brown 1999).

Feeding Stations.—Twenty feeding stations in areas with vegetation that provided many potential perching sites were established for behavioral observations within the boundaries of the field station. This increased the probability that arthropod foraging could be observed in conjunction with nectar foraging. Each individual feeding station consisted of either a Perky-Pet Glass Feeder (Model No. 203-CP, Woodstream Corp., Denver, CO, USA) with the perch and corolla removed, or a triplet feeder constructed from three smaller Perky-Pet plastic singlet feeders (Model No. 214, Woodstream Corp., Denver, CO, USA) connected with Velcro® strips. The feeders were suspended from either a tree branch or a wire hook attached to a vertical length of PVC pipe. The height of the feeders (distance from the ground to the bottom of the feeder) ranged from 0.74 to 2.10 m. A 0.52 M (18% weight/weight) sucrose solution, a concentration typical of nectars in many hummingbird flowers (Baker 1975), was used at all the feeding stations.

Observations were made at four different time intervals for 97 hrs throughout the day during June and July 1998 and 1999. The timed intervals were: early morning (0500–0730 hrs MST), late morning (0800–1130 hrs), late afternoon (1500–1800 hrs), and early evening (1815–1930 hrs). The time of day each feeding station was visited was randomized to ensure an unbiased examination of both nectar and arthropod foraging over all times of day in all habitat types.

Arthropod Foraging.—The amount of time birds spent foraging for arthropods near the feeding stations was recorded. Arthropod foraging was divided into two modes: perch foraging and aerial foraging. Foliage gleaning or other known modes of arthropod foraging (Stiles 1995) were not detected. Perch foraging occurs when birds forage for arthropods while sitting on a perch (no flight is involved). This mode of arthropod foraging has been noted in a few hummingbird species (Pitelka 1942, Brice 1992). Typical behaviors include tongue extension, the bill opening, ''gulping'', or the head darting back and forth. Arthropod foraging data were only taken when it was clear that birds were attempting to catch arthropods (often the vantage point made it possible to see arthropod capture). Time spent perch foraging was measured by starting a stopwatch when a bird opened its bill, extended the tongue, or when the bird gulped (indicating the initiation of an arthropod foraging bout). The

number of attempts the bird made for arthropods was counted with the stopwatch running and the measurement was terminated when the bird flew, vocalized, scratched, rubbed its bill, preened its feathers, or lost active interest. The approximate height of the perch where the event occurred was recorded after recording the time and the number of attempts.

The second major mode of arthropod foraging, aerial flycatching, occurs during hovering or slow forward flight (Stiles 1995). We measured the duration of aerial flycatching bouts with a stopwatch from the time the bird left its perch until it returned to a perch or when the bout had clearly ended. The number of foraging attempts during a bout was estimated (we could not reliably count actual captures) by counting the number of head lunges (indicating a capture attempt). The height of the perch from which the bout was started was estimated visually.

Crop and Gizzard Analysis.—Crop and gizzard data came from samples taken by dissection of 17 birds ($n = 5$ *L. clemenciae*, $n = 6$ *E. fulgens*, and $n = 6$ *A. alexandri*) during June and July 1996. Gut contents were preserved in 95% ethanol. Whole or nearly whole arthropod specimens were identified to the lowest possible taxon. Measurements of the length of whole arthropods were made to calculate an approximate size range for arthropod prey. The crop and gizzard contents were dried to a constant mass in a drying oven (65° C) so we could compare the relative mass of arthropod contents for each hummingbird species.

Measurements were standardized to compare the amount of arthropod material in the gut between species by dividing the mass of arthropod material collected by bird metabolic body mass ($g^{0.75}$; the exponent approximately describes the relationship between body mass and metabolic rate; Calder and King 1974).

Gut Allometry.—The gut mass and length of each species were compared with 10 and eight other hummingbird species, respectively (M.-V. López-Calleja, C. Martínez del Rio, and J. E. Schöndube, unpubl. data). The intestines, from proventriculus to cloaca, were removed from birds killed by thoracic compression and immediately placed in 1.02% saline. The intestine was flushed with saline, blotted dry, and weighed to the nearest 0.01 g after any fat and mesentery were removed. Total length was measured to the nearest 0.1 mm with a digital caliper after the intestine was gently straightened. The relationship between gut length, gut mass, and body mass was examined using standard linear least-squares regression as well as phylogenetically independent contrasts (PIC; Felsenstein 1985, Garland et al. 1992). We performed least-squares regressions of log gut mass versus log body mass and log gut length versus log body mass for standard analysis. We calculated PIC for log body mass, log gut mass, and log gut length (Garland et al. 1992). The phylogeny and relative branch lengths used in our PIC analysis were based on McGuire et al. (2007) and Garcia-Deras et al. (2008) (Fig. 1). The maximum branch length was arbitrarily set at 1.0 with shorter branch lengths scaled appropriately. PIC analysis is robust to branch length variation (Garland et al. 1999) and setting branch lengths in this manner are unlikely to influence PIC results. Absolute values of standardized contrasts were correlated with their branch lengths, and branch lengths were increased by a factor of 10 and log transformed. This made correlations non-significant and contrasts were

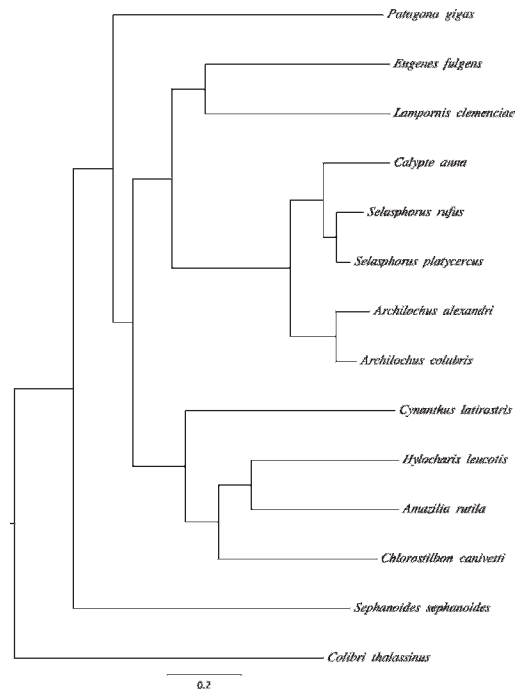

FIG. 1. Presumed phylogeny of 14 hummingbird species used in our phylogentic independent contrasts. A 0.2 branch-length scale is below the physlogenetic tree. The phylogeny is based on McGuire et al. (2007) with placement of *C. latirostris* based on García-Deras et al. (2008).

weighted equally in subsequent analyses. Standardized contrasts were positivized according to Garland et al. (1992). We performed least-squares regression through the origin on positivized contrasts of log gut mass versus log body mass and log gut length versus log body mass.

Respiratory Quotient.—Respiratory quotient (RQ) measures the proportion of carbohydrate fuel an animal catabolizes during the measurement process by comparing carbon dioxide production with oxygen consumption ($RQ = Vco_2/Vo_2$). A measurement close to 1.0 represents pure carbohydrate use, while for birds an RQ close to 0.7 represents pure protein/fat use. Comparing RQs between species provides a view of the importance of nectar as a fuel at a given point in time. A bird foraging more on arthropods might be expected to have an RQ closer to 0.7. We predicted RQs for wild-caught *E. fulgens* would be lower than those for the other two species.

Birds were captured in mist nets three times each day (morning, midday, and late afternoon) and randomly assigned to one of two groups: (1) those caught from the wild and not fed, and (2) those birds that were fed sucrose solution after being caught but prior to RQ measurements. Fed birds were allowed to drink their fill of 0.86 M sucrose solution, and served as a control because they were presumably catabolizing primarily carbohydrate. The RQ of unfed individuals was expected to reflect the ''normal'' metabolic substrate for a bird at a certain time of day.

Measurements of O_2 consumption (Vo_2) and CO_2 production (Vco_2) were made using an open-circuit, positive-pressure respirometry system (Powers 1991). Body mass was measured to the nearest 0.1 g both before and after trials using a portable balance (Model No. LS 200, Ohaus Corp., Pine Brook, NJ, USA). The birds for each trial were kept for about 0.5 hr in a metabolism chamber within an environmental chamber at a constant temperature (27°C) prior to making measurements. Metabolism chambers consisted of a large Mason jar (effective volume: 800 ml) for *E. fulgens* and *L. clemenciae* or a small Mason jar (effective volume: 380 ml) for *A. alexandri*. Metabolism chambers were placed in an environmental control chamber (I-35L, Percival Scientific, Perry, IA, USA). Temperatures were recorded to the nearest 0.1°C using a Physitemp Bat-12 (Physitemp Instruments, Clifton, NJ, USA) and a Cu-Cn thermocouple. The flow rate of dry, CO_2-free air through the metabolism chamber was 500 ml/min. The inlet air passed through soda lime and Drierite to remove ambient CO_2 and water vapor, respectively, prior to passing through an O_2 analyzer (Model No. S-3A, Applied Electrochemistry, Naperville, IL, USA) and a CO_2 analyzer (Model No. LI-6262, LI-COR Biosciences, Lincoln, NE, USA). Data acquisition and analysis were with a Power Macintosh (Model No. 7200, Apple Computer Corp., Cupertino, CA, USA) using Warthog LabHelper and LabAnalyst software (Mark Chappell, University of California, Riverside, CA, USA).

Statistical Analysis.—We used nonparametric analysis of variance (Kuskal-Wallis test; Zar 1974) to evaluate differences among sample means. *Post hoc* testing was by multiple comparisons using Mann-Whitney *U*-tests (Zar 1974) when more than two groups were compared with alpha values adjusted using the Bonferroni correction. Curves illustrating allometric relationships were plotted using simple linear regression and the extent of variation explained by the regression is reported as r^2 (Zar 1974). All statistical calculations used SPSS 16.0.1 (SPSS 2007). Values reported are means ± SD.

RESULTS

Arthropod Foraging.—Individual *A. alexandri* were difficult to locate and observe foraging for arthropods, possibly because the presence of one or more aggressive *L. clemenciae* motivated these birds to remain inconspicuous. *E. fulgens* and *L. clemenciae* both exhibited a higher arthropod foraging rate aerially than while perched (*E. fulgens*: $U_{1,81} = 21.5$, $P < 0.001$; *L. clemenciae*: $U_{1,81} = 27.9$, $P < 0.001$; Fig. 2). *E. fulgens* had a higher aerial foraging rate than *L. clemenciae* ($U_{1,113} = 4.8$, $P = 0.03$). *L. clemenciae* perhaps compensated for the lower aerial foraging rate by spending more time in areal foraging than *E. fulgens* ($U_{1,25} = 6.93$, $P = 0.01$; $\bar{x} = 0.09 \pm 0.1$ min/hr for *E. fulgens*, $\bar{x} = 0.52 \pm 0.6$ min/hr for *L. clemenciae*). The majority of individual *E. fulgens* engaged in aerial arthropod foraging (87% of 93 observations) rather than perch foraging (13% of 93 observations). Individual *L. clemenciae*, in contrast, divided arthropod foraging activity more evenly with 45% engaged in perch foraging and 55% foraging aerially (95 total observations). These birds would typically drink from a feeder and then perch in close proximity to the feeder. *L. clemenciae* would often engage in

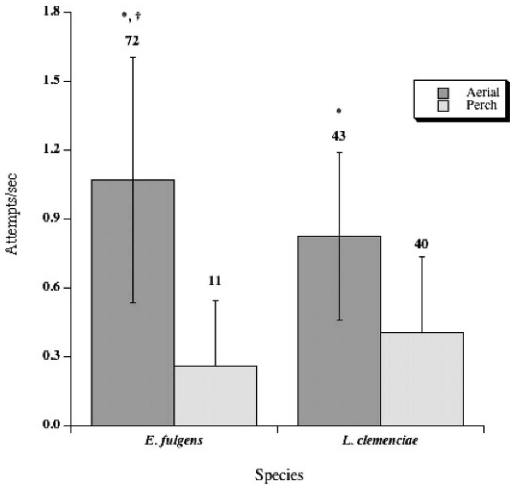

FIG. 2. Mean (± SD) number of insect capture attempts per second for *E. fulgens*, and *L. clemenciae* during a foraging bout. Numbers above the error bars are sample sizes. The ''*'' indicates a significant difference between the aerial and perch values for both *E. fulgens* and *L. clemenciae*. The ''†'' indicates a significant difference between aerial values for *E. fulgens* and *L. clemenciae*.

this behavior for a short time and then fly to defend the nearest feeder or to feed from it.

There was a marked difference in the average height from which the two species foraged for arthropods with *E. fulgens* perching at a greater height in both modes than *L. clemenciae* (aerial foraging height $U_{1,81} = 32.2$, $P < 0.001$; $\bar{x} = 9.9 \pm 4.7$ m for *E. fulgens*, $\bar{x} = 3.6 \pm 2.5$ m for *L. clemenciae*; perch foraging height: $U_{1,37} = 5.23$, $P = 0.02$; $\bar{x} = 5.9 \pm 4.0$ m for *E. fulgens*, $\bar{x} = 2.1 \pm 1.2$ m for *L. clemenciae*). Both species engaged in aerial foraging from a higher perch than when perch foraging (*E. fulgens*: $U_{1,59} = 5.39$, $P = 0.02$; *L. clemenciae*: $U_{1,59} = 5.84$, $P = 0.02$). *E. fulgens* appeared to remain high in the tree canopy (especially in *Juglans* spp. and *Platanus* spp.), while *L. clemenciae* perched in lower tree limbs or understory shrubs where it was closer to feeders.

Crop and Gizzard Contents.—Guts of *E. fulgens* contained the most arthropod taxa of our three study species (Table 1). The number of taxa represented (from 2 Classes and 4 Orders) is conservative because only arthropods that could be positively identified (to the lowest possible taxon) are reported. This meant identifying nearly whole specimens only. Absolute number of individuals in each of the taxa could not be calculated because most ingested arthropods were fragmented. All three identifiable members of the Order Hymenoptera were wasps. Several Homopteran specimens were the same type of leafhopper (Family Cicadellidae). There were three insects and one arachnid specimen that could not be further identified.

Numbers and size range of whole arthropods as well as the dry mass of all arthropod material collected from the three hummingbird species digestive tracts did not differ (dry mass: $H_{2,16} = 2.096$, $P = 0.351$; whole arthropods: $H_{2,16} = 2.228$, $P = 0.328$; Table 2).

Gut Allometry.—The linear regressions of gut mass and body mass, and the phylogentically independent contrasts (PIC) of gut mass and body

TABLE 1. Arthropod taxa found in crops and gizzards of hummingbird species in this study.

Species	A[a]	B[a]	C[a]	D[a]	E[a]	F[a]	G[a]	H[a]	I[a]
E. fulgens	X		X	X	X		X	X	X
L. clemenciae	X	X		X		X			
A. alexandri	X		X						X

[a] A = Class Insecta, Order Hymenoptera (length 3.4 – 5.8 mm); B = Class Insecta, Order Hymenoptera (length 2.5 mm); C = Class Insecta, Order Hymenoptera (length 1.0 mm); D = Class Insecta, Order Homoptera, Family Cicadellidae; E = Class Insecta, Order Diptera; F = Class Insecta (unknown Order[b]); G = Class Insecta (unknown Order[b]); H = Class Insecta (unknown Order[b]); I = Class Arachnida, Order Araneae.
[b] Different from other listed categories.

TABLE 2. Arthropods ($\bar{x} \pm$ SD) in crops and gizzards of hummingbirds in this study.

Species	*n*	Whole arthropods (#/individual)	Arthropod length (range, mm)	Dry mass (mg/g$^{0.75}$)
L. clemenciae	5	1.8 ± 3.0	2.47–2.55	0.9 ± 1.2
E. fulgens	6	6.2 ± 7.3	1.02–5.75	1.6 ± 1.6
A. alexandri	6	0.8 ± 1.1	0.97–3.50	1.6 ± 1.0

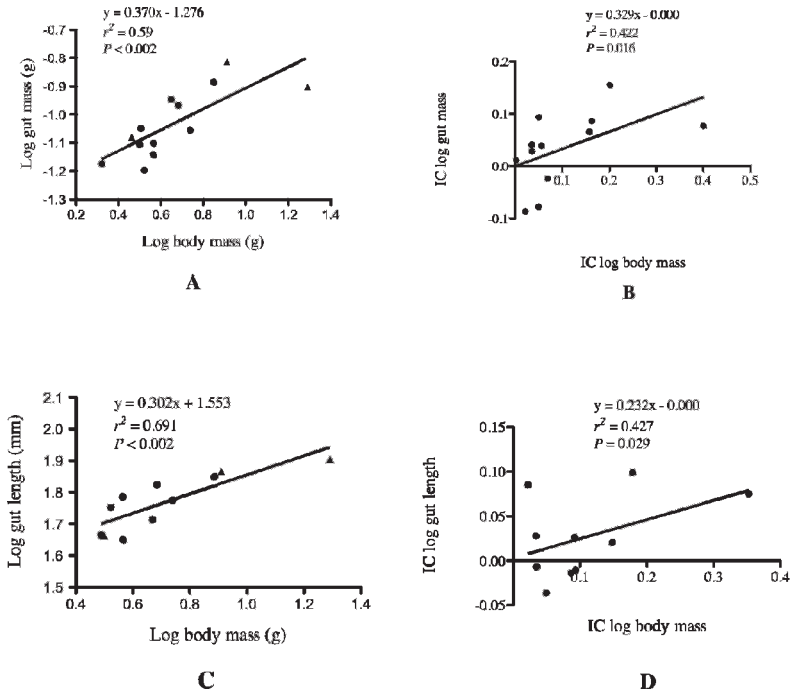

FIG. 3. The relationship between gut mass and length, and body mass in hummingbirds ranging in size from ~2 to 20 g. A and B are the standard linear regression and the linear regression of independent contrasts for gut mass as a function of body mass. C and D are the standard linear regression and the linear regression of independent contrasts for gut length as a function of body mass. Triangles in A and C are hummingbird species in this study.

mass were both significant (Fig. 3A, B) indicating body mass is a key factor affecting gut mass. The linear regression and PIC of gut length and body mass was also significant (Fig. 3C, D) indicating gut length varied with body mass.

Respiratory Quotient.—Respiratory quotient (RQ) within a species did not vary with time of day and the data for each species were pooled (Fig. 4). There was no difference between fed and unfed RQ for *A. alexandri* ($U_{1,16} = 2.91$, $P = 0.09$). There was a difference between fed and unfed RQ for both *E. fulgens* and *L. clemenciae* (*E. fulgens*: $U_{1,19} = 13.7$, $P < 0.001$; *L. clemenciae*: $U_{1,19} = 12.39$, $P < 0.001$). *E. fulgens* also had a lower unfed RQ than *A. alexandri* or *L. clemenciae* ($H_{2,39} = 6.88$, $P = 0.032$). There was little variation in unfed RQ in *E. fulgens*.

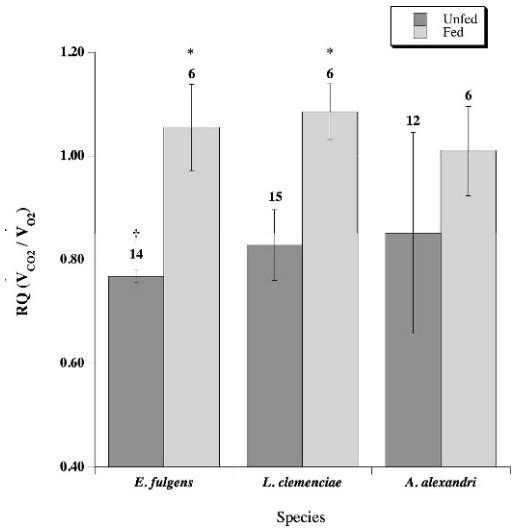

FIG. 4. Fed and unfed mean (± SD) respiratory quotient (RQ) for *A. alexandri*, *E. fulgens*, and *L. clemenciae*. The ''*'' indicates a significant difference between fed and unfed birds of the same species. The ''†'' indicates significance between unfed RQ for *E. fulgens* and the other species.

DISCUSSION

Nectar carbohydrates have been assumed to be the primary energy source for hummingbirds, but arthropods may also provide significant amounts of energy in addition to protein and lipids. Most insects from sweep net samples (Weathers and

Sullivan 1989) conducted in the Chiricahua Mountains were from the Orders Coleoptera, Homoptera, and Diptera. Weathers and Sullivan (1989) showed these insects have an average energy value of about 25 kJ/g (dry mass). Karasov's (1990) conservative estimate of the metabolizable energy of insets is 19.3 kJ/g (dry mass) compared to 16.4 kJ/g for nectar. Thus, energetically, arthropods have the potential to be more than a small supplement to a primarily carbohydrate diet. Hainsworth (1977) showed that if a hummingbird devotes equal time to nectarivory and flycatching, even low efficiency rates of ~40% can provide more energy than nectar feeding.

E. fulgens seemed to emphasize aerial foraging for arthropods. They spent the vast majority of their arthropod foraging time in this mode, had the highest frequency of capture attempts, and generally foraged from higher perches. *L. clemenciae* split their time more evenly between perch and aerial foraging, but actually spent more total time foraging for arthropods. It is possible that we actually observed a relatively small portion of their total arthropod-foraging activity because of the traplining behavior of *E. fulgens*.

Sandlin (2000a) suggested that *E. fulgens* switches to arthropod foraging to avoid the consequences of competition. Successful territorial species such as *L. clemenciae* maintain reliable nectar sources by defending them from invaders thereby gaining an energetic advantage (Powers et al. 2003). Thus, *L. clemenciae* may prefer to perch close to feeders, facilitating quick responses to intruders. This would be an efficient way to supplement their nectar diet for *L. clemenciae* foraging on arthropods while perched in a defensive position. Powers and Conley (1994) report that *L. clemenciae* are perched about 70% of the time, allowing them to both guard their territory and to forage for passing insects when available.

E. fulgens had the greatest diversity of arthropod species in its crop and gizzard (Table 2). These data corroborate the findings of Cottam and Knappen (1939) who examined gut contents of *E. fulgens* and *L. clemenciae* from the nearby Huachuca Mountains of Arizona. They found 13 different taxonomic specimens in the guts of *E. fulgens* but only seven in *L. clemenciae*. The reason for this difference is unclear. *E. fulgens* forages for arthropods higher in the canopy than *L. clemenciae* and the greater arthropod diversity in *E. fulgens* guts may reflect the diversity of arthropods available in the upper canopy. It is also possible the trapline-foraging behavior of *E. fulgens* diversifies the arthropod component of the diet (Colwell 1973, Feinsinger and Chaplin 1975). Our data show that *E. fulgens* and *L. clemencae* forage differently for arthropods but there is no evidence for a difference in arthropods consumed.

It is not possible to calculate the total contribution of arthropods to the diet of the hummingbirds in this study. It has been suggested the types of arthropods we found in the guts are digested quickly (Remsen et al. 1986, Stiles 1995). Thus, our measures of dry mass are probably a good index of short-term arthropod consumption and correspond reasonably well to the maximum rate arthropods were captured (range ~6 to 30 captures/hr assuming 100% capture efficiency and total arthropod digestion in 1 hr). The total digestible energy of arthropods consumed ranges from 0.2 to 0.4 kJ/day if arthropod dry mass is turned over in the gut hourly. Daily energy expenditure (DEE) is 82 kJ/day for *L. clemenciae* and 29 kJ/day for *A. alexandri* (Powers and Conley 1994). Our data suggest arthropods account for <1% of DEE assuming DEE for *E. fulgens* is similar to *L. clemencae*. These data suggest there is no difference in arthropod consumption or energy derived from arthropods for our three hummingbird species.

Our hummingbirds had gut masses and lengths that corresponded with their body size suggesting that none of the hummingbirds in this study has a unique gut design. Any ability to subsist on arthropods when nectar is scarce is likely a common trait in hummingbirds.

All three hummingbird species had RQ values <0.85 indicating they were not strictly catabolizing carbohydrate. The RQ of *E. fulgens* was statistically lower than the other two species but we are uncertain if the difference is truly enough to argue a difference in use of arthropods for energy. The low variability in *E. fulgens* RQ does at least hint at a difference in how the three species forage but the exact nature of this difference is unclear. The higher variability in the RQ of *L. clemenciae* and *A. alexandri* could correlate with time since their last nectar meal. The lower variability in *E. fulgens* could support more consistent arthropod consumption but it could also be explained by the routine capture of

traplining individuals that have not yet fed. RQ data alone are insufficient to draw conclusions regarding the importance of different metabolic substrates used by the hummingbirds in this study. Hummingbirds can rapidly switch between fatty acid and carbohydrate oxidation (Welch and Suarez 2007) making interpretation of a depression in RQ difficult.

E. fulgens differs behaviorally in arthropod foraging from at least *L. clemenciae* but there is no strong evidence that arthropod consumption provides a disproportionate amount of energy compared to the other hummingbird species in this study. It is probable that all three species energetically benefit from arthropods but quantifying the total contribution of insects to their energy budget is difficult. We still do not have a complete understanding of the role arthropods have in hummingbird nutrition but are hopeful that future studies using techniques such as stable isotope analysis might provide addition insight.

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