

THE EFFECT OF FOOD AVAILABILITY ON TIME AND ENERGY EXPENDITURES OF TERRITORIAL AND NON-TERRITORIAL HUMMINGBIRDS¹

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Abstract. We studied the time and energy allocations related to territorial behavior in male Blue-throated Hummingbirds (*Lampornis clemenciae*; about 8.3 g) under conditions of unlimited and restricted food availability. When food was unlimited, territorial males avoided inter-specific aggression, chasing only 11% of the inter-specific intruders (Black-chinned Hummingbirds, *Archilochus alexandri*; about 3.5 g). Thus, when food was unlimited, inter-specific intruders were able to forage efficiently, meeting their estimated daily energy requirement with ease (27 kJ/day). Conversely, 81% of intra-specific intruders were chased, and intra-specific intruders were able to feed at territorial feeders only when the territorial male was away. Chases of intra-specific intruders were longer and appeared to be more intense than chases of inter-specific intruders. When food was restricted territorial activity, including the total number of chases engaged in by the territory owner, was significantly reduced, although the basic characteristics of territorial behavior (e.g., chases and displays) did not change. Territory owners chased a higher proportion of inter-specific intruders when food was restricted (48%), suggesting an increase in inter-specific competition. A high proportion of intra-specific competitors continued to be chased (80%), although the total number of intra-specific intruders was lower. We believe that variations in the cost of territoriality are dependent primarily on the level of intra-specific competition. This is supported by the fact that when food was restricted to an amount that could support a maximum of 1.4 *L. clemenciae* (based on doubly labeled water measurements of field metabolic rate in a previous study), energy intake by the territory owner decreased from 114 kJ/day to 64 kJ/day, with the primary difference being number of intra-specific chases. These data also suggest that the exclusion of other hummingbird species might be based strictly on the amount of available food (energy). When food is restricted, inter-specific competition is more costly to the territory owner causing the exclusion of a higher proportion of inter-specific intruders. The high proportion of intra-specific intruders that are chased in either experimental condition suggests that territorial behavior in *L. clemenciae* might have functions other than resource protection per se, such as social functions related to their mating system.

Key words: *Archilochus alexandri*; *Lampornis clemenciae*; *Trochilidae*; territoriality; food resource limitation.

INTRODUCTION

Animals rarely exist under conditions of unlimited food (energy) availability. Because an adequate supply of food is vital for survival, animals often exhibit behaviors (frequently involving aggression) that insure access to food in a given area. An example of such behavior is territoriality, which is presumed to be adaptive when the benefits of exclusive use of an area or other resource (e.g., food) exceed the cost of defense (Brown 1964, Carpenter and MacMillen 1976). This economic analysis of territorial behavior is largely based on studies of feeding territories (territories defended during the non-breeding sea-

son) because their characteristics are presumably tied to the density and distribution of a specific resource, primarily food (e.g., Carpenter and MacMillen 1976, Kodric-Brown and Brown 1978). However, many animals that exhibit territoriality defend resources other than food and in some cases appear to tolerate, at least over the short-term, an energy deficit (e.g., trout and pupfish during the breeding season; Feldmeth 1983). It is also important to note that, in territorial systems where this occurs, the importance of behaviors that are prioritized above energy acquisition is not always obvious. For example, Powers and Conley (1994) in a study of Blue-throated Hummingbirds (*Lampornis clemenciae*) concluded that although territorial males exhibited the classic behavior of hummingbirds defending

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feeding territories, the dynamics of their territorial system was likely driven to a large degree by intra-specific social interaction. Their conclusions were based on the fact that territorial males did not defend their food source efficiently and because strong aggression was exhibited only towards conspecifics. Examples such as this underscore the importance of not assuming a territorial system is strictly energy based because a food source is defended. Rather, an understanding of territorial dynamics should be based on a complete analysis of the important behaviors and the energetics of the organism involved.

Hummingbird energetics has been of interest to biologists for some time, as evidenced by the many papers published on the subject. A large proportion of these studies have included estimates of the energy costs associated with foraging (e.g., Ewald and Carpenter 1978, Wolf 1978), with the primary focus being on territorial species. To guarantee a high energy intake, many hummingbirds forage at and defend quality food sources (i.e., feeding territories), which involves making frequent short flights to feed, chasing intruders, and performance of aggressive displays (e.g., Stiles 1971, Kodric-Brown and Brown 1978). Other hummingbird species, however, are non-territorial, and rarely engage in aggressive defense. Examples of non-territorial hummingbirds include subordinate species that are excluded from food sources (e.g., Pimm et al. 1985), and traplining species that forage over a wide area (Feinsinger 1986). These species undoubtedly work hard to meet their energy demands because of higher foraging costs (Wolf 1978). Territorial species are easier to work with because their activities are generally confined to a specific area, whereas non-territorial hummingbirds can be widely scattered and less predictable. Thus, few empirical data are available on non-territorial hummingbirds, which limits our understanding of their energetics and makes direct comparisons with territorial species difficult. Comparisons that might be attempted between territorial and non-territorial hummingbirds are also complicated by differences in the thermal environment (e.g., conductive, convective, and radiative heat transfer) experienced by individual species which can have a significant impact on field metabolic rate (FMR) (e.g., Bakken 1976).

It is becoming increasingly clear that hummingbird behavior is influenced by the distribution of food (energy) resources. For example,

breeding male Anna's Hummingbirds (*Calypte anna*) and Calliope Hummingbirds (*Stellula calliope*) modified their foraging behavior as food distribution changed, yet they kept other aspects of their behavior constant (Armstrong 1987, Powers 1987). These behavioral changes include aggressive activities against competitors as well as direct foraging activities. Thus, changes in food quality and distribution impact behaviors that contribute to FMR. This might explain Powers and Conley's (1994) observations of *L. clemenciae* and the Black-chinned Hummingbirds (*Archilochus alexandri*) during conditions of unlimited food availability, where *L. clemenciae* essentially abandoned inter-specific territoriality, and focused solely on conspecific interactions. Because of this *A. alexandri*, a non-territorial forager where they coexisted with *L. clemenciae*, was in some cases able to remove more energy from territorial feeders than the territory owners. In addition, doubly labeled water measurements suggest that under these conditions *A. alexandri* had a much lower FMR than the larger *L. clemenciae*. *Archilochus alexandri* was therefore able to operate at a higher energetic efficiency as a non-territorial forager than the territorial *L. clemenciae*.

The next logical step in examining the relative cost of territorial vs. non-territorial foraging in hummingbirds is to determine if changes in foraging behavior and relative foraging costs occur when food supplies are restricted. To test the effects of energy restriction, we used the sympatric populations of *L. clemenciae* and *A. alexandri* described above. We hypothesize two possible outcomes: (1) *L. clemenciae* will continue to be aggressive against conspecific intruders, but will exclude a higher proportion of inter-specific intruders, or (2) both species will alter their foraging behavior in order to adapt to new levels of food availability (e.g., Stiles 1971 vs. Powers 1987). If the first hypothesis is correct, then territoriality with regard to conspecifics is obligatory for *L. clemenciae* and probably evolved in response to selective pressures other than just the need to protect a food source (e.g., position in a lek; see Kuban and Neill 1980). In this case, *A. alexandri* should be forced to forage in other areas (presumably at a higher cost) as suggested by Pimm et al. (1985), and their densities in the study area should decrease. If the second hypothesis is correct, then the dynamics of the *L. clemenciae* territorial system should be similar

to that described by standard cost-benefit models. In this case foraging costs of both species would likely be higher due to the increased cost of finding food. Determining which of the above hypotheses are correct will provide insight into the evolution of territoriality in hummingbirds and the degree to which these species can adapt to different or changing environments.

METHODS

STUDY AREA

We conducted our study during June 1991 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; altitude 1,700 m). The riparian habitat surrounding the station is bordered by oak woodland and a mixed deciduous/coniferous forest. For a more complete description see Pimm (1978). Small insects of a size presumably suitable as hummingbird prey were abundant during the study.

EXPERIMENTAL PROTOCOL

Four locations at the Southwestern Research Station (SWRS) were supplied with a feeder around which birds could establish territories. Feeders were located approximately 100 m apart. Each feeder consisted of four 12-mL syringes (Monoject #512910) with regular Luer slip tips. The tips of the syringes were cut off to slightly enlarge the hole and painted red with nail polish. Syringes were filled with 20% sucrose solution (1.0 g sucrose mixed with 4.0 g water). Syringes were inserted through a Plexiglas® plate suspended from an aluminum pole.

Two conditions of food (sucrose solution) availability were used: (1) unlimited, i.e., food was always available, and (2) restricted, where each territory was provided with only 32 ml of sucrose solution per day, an amount equal to about 114 kJ/day (assuming 0.216 g sucrose/ml and 16.5 kJ/g sucrose; Weast et al. 1983). The amount of energy provided in the latter condition exceeded the energy needs of a single *L. clemenciae* (82 kJ/day based on doubly labeled water measurements; Powers and Conley 1994) by 39%, which provided opportunity for successful intrusion. When food was restricted 20 ml (71 kJ) of sucrose solution was added to the feeders at 04:30 hr, which was before the birds became active, and 12 ml (43 kJ) at 15:00 hr.

Providing nectar in this manner more closely mimics nectar production in natural flowers, which is often somewhat bimodal, with nectar production high in the morning and a second smaller peak in the afternoon (e.g., Stiles 1975). During the first half of this study all territories were food restricted whereas all territories had unlimited food during the second half of the study.

Energy and time costs during the active period for both the territory owner (*L. clemenciae*) and intruders (*A. alexandri*), and energy resource management by the territory owner, were evaluated using time-budget analysis, territorial food depletion measurements, and measurements of feeding rate. The hummingbirds' active period was divided into three parts: morning (05:00 hr to 09:00 hr), midday (10:00 hr to 15:00 hr), and evening (16:00 hr to 19:00 hr).

TIME BUDGETS

We measured time budgets on individual territorial *L. clemenciae* males defending each of the four experimental feeders and intruding *A. alexandri*. All territorial *L. clemenciae* and many of the intruders could be identified by color markings on their backs (see Powers and Conley 1994). Because we could not identify each of the intruders, the impact of individual intruders could not be assessed. Fifty hours of time budget per species were obtained during each experimental manipulation of food availability. Time budgets were assessed by positioning an observer approximately 20 m from the territorial feeder, with frequency and duration of specific activities recorded for both species. Activities measured for *L. clemenciae* were perching, nectar feeding, chasing, miscellaneous flight, and out-of-sight time. Chasing was subdivided into two categories: intra-specific and inter-specific. Miscellaneous flight included flights around the territory not associated with feeding or chasing. Flycatching was also 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 could not be seen by the observer. Time budget data for *L. clemenciae* were recorded with a TRS 100 lap-top computer (Tandy Corp.). Activities recorded for *A. alexandri* were nectar feeding and chasing. Timed activities for *A. alexandri* were recorded using stop watches. Time budgets were recorded between 05:00 hr and 19:00 hr during 1-hr observation periods. Schedules were deter-

mined in advance with time, territory, and observer selected randomly. For convenience, time budget observations always started on the hour.

NECTAR CONSUMPTION

To track patterns of food removal from the experimental territories nectar depletion from the territorial feeders was recorded each hour during the hummingbirds' active period. Changes in feeder volumes were recorded to the nearest 0.2 ml. Syringe volumes were calibrated by measuring the mass of a volume of water inside the syringe. Feeders were initially filled each day prior to the beginning of the active period, and the final feeder measurement taken after the hummingbirds had gone to roost.

FEEDING RATE

To estimate energy intake we measured feeding rate for each hummingbird species. The feeder used in these measurements was located outside our laboratory window because the apparatus could not be operated at territory sites. The feeders used, however, were identical to those in the experimental territories. 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. Calibration was checked regularly to insure the accuracy of our measurements. Output from the strain gauge was sampled at 0.5 sec intervals with a Campbell Scientific CR21X data-logger.

TEMPERATURE MEASUREMENTS

We monitored temperature each day of the study in an unsheltered area near the feeding stations 3 m above the ground. Shaded ambient temperature (T_a) was measured with a 24-gauge Cu-Cn thermocouple and operative temperature (T_e ; Winslow et al. 1937), a temperature increase or decrease due to radiative and convective factors, with a copper sphere thermometer painted flat-gray (Walsberg and Weathers 1986). Output from the thermocouple and sphere thermometer was sampled every minute and averaged every 15 min by a Campbell Scientific CR21X datalogger. We measured precipitation with a rain gauge

maintained by the station. All measurements, except for rain amounts, were made continuously (24 hr/day) throughout the study.

STATISTICS

Sample means were compared using paired and unpaired Student-*t* tests when appropriate (Zar 1974). Comparison of morning, afternoon, and evening samples was done using the Kurskal-Wallis test (Zar 1974). Results are given as the mean \pm one standard deviation. Differences are considered significant if $P < 0.05$.

RESULTS

WEATHER

Minimum T_a occurred at 05:00 hr and averaged $9.8 \pm 2.0^\circ\text{C}$. Minimum T_e also occurred at 05:00 hr and was significantly lower than minimum T_a ($t = 9.84$, $df = 19$, $P < 0.05$) averaging $8.9 \pm 2.8^\circ\text{C}$. Maximum T_a occurred at 15:00 hr and averaged $28.0 \pm 5.9^\circ\text{C}$. Maximum T_e also occurred at 15:00 hr and was significantly higher than maximum T_a ($t = 23.51$, $df = 27$, $P < 0.05$) averaging $33.8 \pm 8.0^\circ\text{C}$. Precipitation during the study totalled 5.55 cm, most of which occurred on 1 June (0.74 cm), 10 June (2.41 cm), and 30 June (2.31 cm).

NON-AGGRESSIVE TERRITORIAL BEHAVIOR

Food availability did not appear to change the basic characteristics of *L. clemenciae* territoriality, although the intensity and frequency of certain behaviors did vary (time budgets are summarized in Table 1; also, see below). Territory owners spent significantly more time out-of-sight when food was restricted than when food was unlimited. *Lampornis clemenciae* spent the greatest amount of time off their territory during the afternoon period of the restricted food condition when feeders often were empty. During this period, OOS time differed significantly from OOS time in the morning and evening ($H = 15.322$, $df = 2$, $P < 0.05$). Time-of-day did not affect OOS time when food was unlimited. When afternoon measurements taken during the restricted food condition are eliminated from the analysis, OOS time during the restricted period is still significantly greater than when food is unlimited ($t = 1.175$, $df = 85$, $P < 0.05$).

Territory owners were observed perching significantly longer when food was unlimited than when food was restricted. When food was re-

TABLE 1. Time budget data for territorial *Lampornis clemenciae*. Values are expressed as min/hr \pm 1 SD.

Territory	Perching	Chasing	Feeding	Misc. flight	OOS
Unlimited	17.82 \pm 8.00	1.09 \pm 1.00	1.04 \pm 0.83	0.41 \pm 0.48	38.34 \pm 18.58
Restricted	9.05 \pm 10.83	0.41 \pm 0.46	0.58 \pm 0.58	0.42 \pm 0.61	45.95 \pm 13.70
<i>t</i>	2.992*	4.279*	3.181*	0.930	2.356*

* Indicates significant difference at $P < 0.05$.

stricted time-of-day had a significant impact on the time observed perching ($H = 15.897$, $df = 2$, $P < 0.05$), with the highest amount of perching observed in the morning and the lowest in the afternoon. Perching time did not vary with time-of-day when food was unlimited.

Miscellaneous flight time did not vary between conditions of food availability and averaged less than 1% of the total time budget. However, miscellaneous flight varied significantly with time-of-day when food was restricted ($H = 14.953$, $df = 2$, $P < 0.05$) whereas there was no time-of-day effect when food was unlimited.

ENERGY INTAKE

When food was unlimited, an average of 10.6 \pm 8.4 ml/hr (37.8 \pm 29.9 kJ/hr) of sucrose solution was consumed by hummingbirds throughout the day (Fig. 1A). Total daily nectar removal from the feeders averaged 158.7 \pm 125.6 ml/day which is equivalent to 484 kJ/day. When food was restricted all 32.0 ml (114 kJ) of nectar placed in the experimental feeders each day was consumed. Because of the manner in which nectar was supplied, a bimodal feeding pattern was imposed (Fig. 1B).

The measured rate of food intake for *Lampornis clemenciae* was 2.22 g of sucrose solution per minute of feeding time. Territory owners fed an average 1.04 min/hr (Table 1), consuming an estimated 2.3 g/hr of sucrose solution. Thus, when food was unlimited, total daily energy intake is estimated to be 113.8 \pm 91.3 kJ/day (assuming 0.2 g sucrose/g sucrose solution). Although energy intake was high throughout the day, intake did decline slightly as the day progressed (Fig. 2A). When food was restricted *L. clemenciae*'s total daily energy intake decreased to 63.8 \pm 63.8 kJ/day, with about 57% of their total energy consumption occurring in the morning (Fig. 2A). *Archilochus alexandri* fed at a rate of 1.14 g/min of sucrose solution for 1.8 min/hr, resulting in an intake rate of 2.1 g/hr of sucrose solution when food was unlimited. This is equivalent to about

104.0 \pm 97.6 kJ/day. Like *L. clemenciae*, energy intake for *A. alexandri* decreased throughout the day when food was unlimited, although the decrease was sharper in *A. alexandri* (Fig. 2B). However, *A. alexandri* still consumed large amounts of nectar from territorial feeders throughout the active period. When food was restricted *A. alexandri* consumed only 27.6 \pm 50.2 kJ/day. Unlike *L. clemenciae*, the bulk of *A. alexandri*'s energy intake from the experimental feeders, about 58%, occurred during the evening (Fig. 2B).

Feeding bouts by hummingbirds were not always continuous. Often hummingbirds would pause one to several times during a single feeding bout. The number of pauses occurring during a feeding bout did not vary significantly between conditions of food availability. *Lampornis clemenciae* paused 0.5 \pm 1.3 times during a feeding bout (range: 0 to 8 pauses per feeding bout). *Archilochus alexandri* paused 1.8 \pm 2.7 times per feeding bout (range: 0 to 14 pauses). Pause rates for the two species are significantly different ($t = 10.15$, $df = 1,236$, $P < 0.05$). There was no significant relationship between the number of pauses occurring during a feeding bout and the amount of nectar consumed for either species. The number of pauses was therefore disregarded in the calculation of feeding rate.

TERRITORIAL AGGRESSION

Unlimited food. Intrusion rate by *L. clemenciae* was 8.0 \pm 5.8 intrusions/hr and for *A. alexandri* 10.8 \pm 9.8 intrusions/hr. *Lampornis clemenciae* intruders were chased at a rate of 6.5 \pm 5.3 chases/hr (81%) whereas *A. alexandri* intruders were chased at a rate of 1.2 \pm 2.4 chases/hr (11%). *Lampornis clemenciae* intruders were able to feed at territorial feeders 40% of the time whereas 76% of the *A. alexandri* intruders were able to feed. The duration of feeding bouts for *L. clemenciae* and *A. alexandri* intruders was 0.07 \pm 1.1 sec and 0.22 \pm 0.22 sec, respectively. Feeding bouts by intruding *L. clemenciae* were particu-

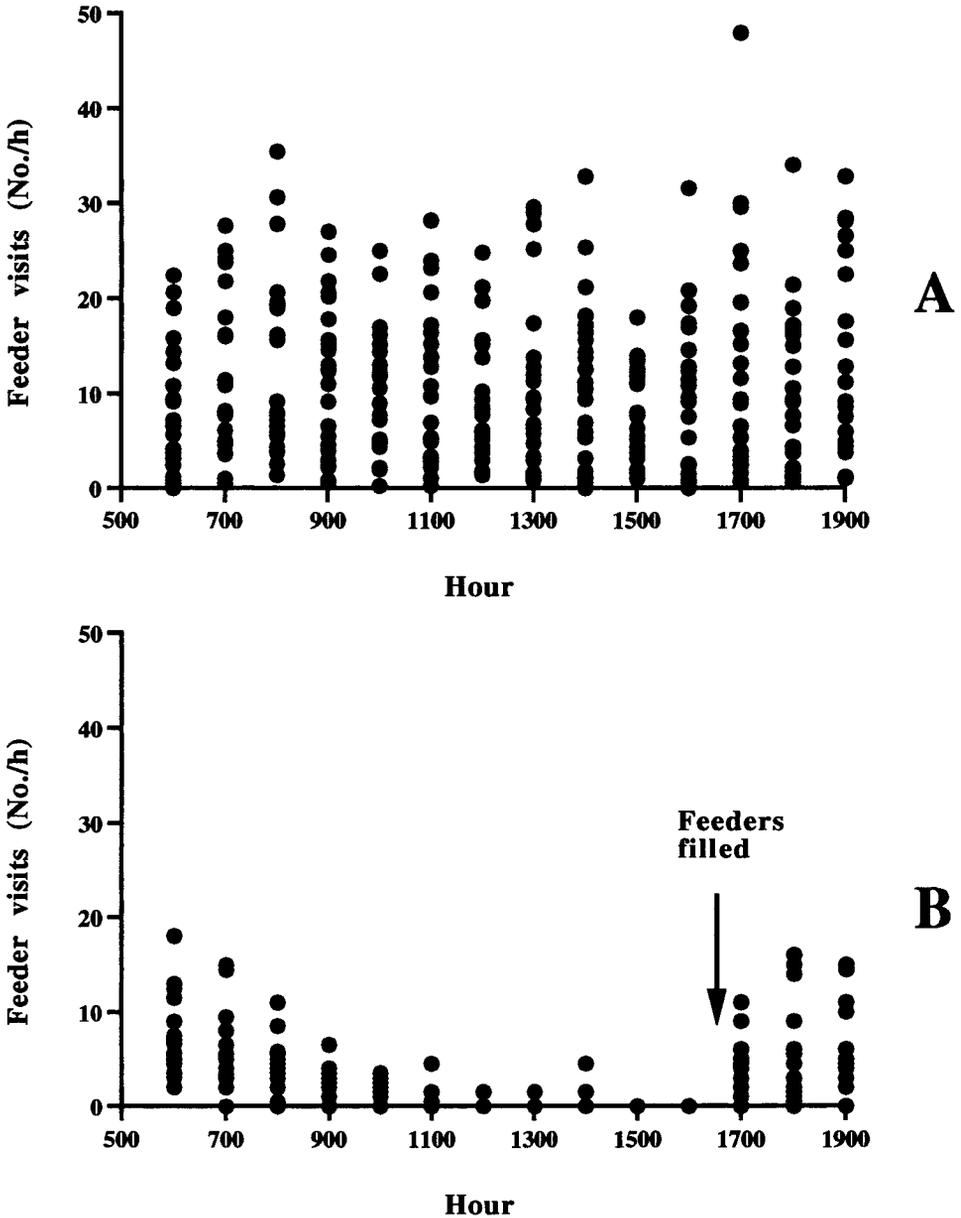


FIGURE 1. Number of times the territory owner visited the territorial feeder A) when food was unlimited and B) when food was restricted. Each point represents the number of feeder visits during an hour observation period.

larly short because the territory owner immediately chased the intruder away from the feeder. Average total time spent chasing intruders was consistent between territories, but variability was high over all time periods. Chases of *A. alexandri* intruders were usually short, lasting only a few

seconds, and terminated several meters from the territorial feeder. Chases of conspecifics, however, could be one to two minutes and appeared to be conducted at higher speeds and with greater intensity than chases of *A. alexandri*. Often *L. clemenciae* other than the territory owner and

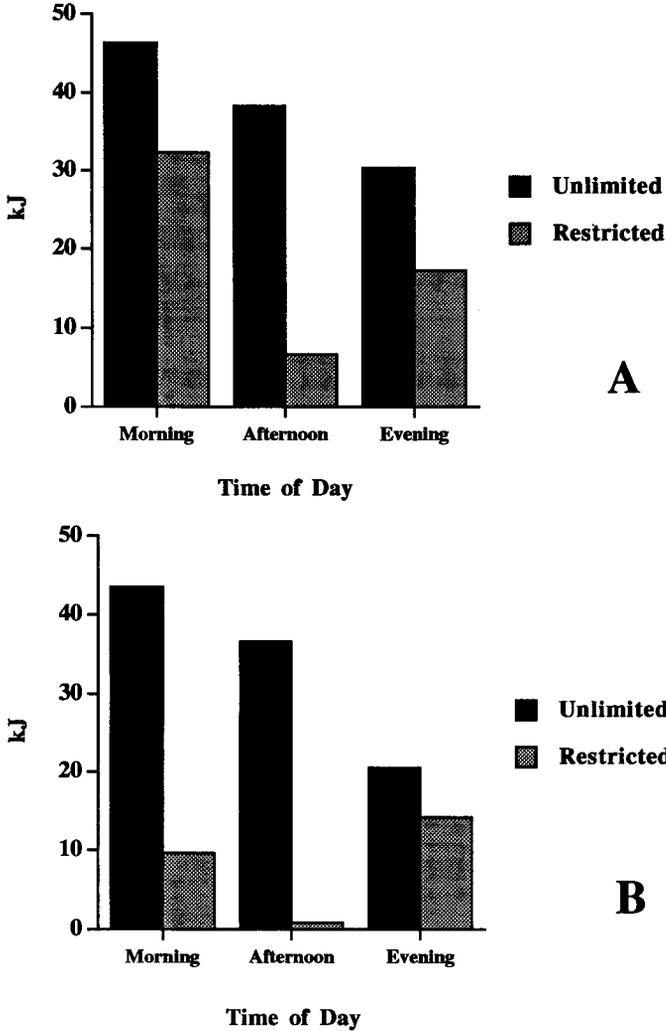


FIGURE 2. The estimated amount of energy consumed from territorial feeders by A) *L. clemenciae* and B) *A. alexandri* during the morning, midday, and evening. Estimation of energy consumption is based on measurements of total feeding time and feeding rate for each of the species.

intruder would participate in chases of intruding *L. clemenciae*. Some chases involved as many as four birds.

Restricted food. *Lampornis clemenciae* intrusion rate decreased to 3.5 ± 4.3 intrusions/hr and *A. alexandri* intrusion rate dropped to 3.6 ± 4.5 intrusions/hr. Both these values are significantly different from the unlimited food condition ($t = 4.499$, $df = 101$, $P < 0.05$ and $t = 4.526$, $df = 101$, $P < 0.05$ respectively). Territory owners engaged in 2.8 ± 3.9 chases/hr (80%) of conspecifics and 1.7 ± 2.6 (48%) chases/hr of *A. alexandri*. Conspecific chases were significantly

less numerous than when food was unlimited ($t = 4.041$, $df = 101$, $P < 0.05$), although territory owners chased the same percentage of intruders. The number of chases of *A. alexandri* did not differ from the unlimited food condition, but territory owners chased a higher proportion of intruders. The proportion of intruders gaining access to the territorial feeders decreased during this portion of the experiment. *Lampornis clemenciae* intruders were able to feed only 29% of the time whereas *A. alexandri* intruders fed only 58% of the time. The duration of intruder feeding bouts was 0.06 ± 1.0 sec for *Lampornis cle-*

menciae and 0.23 ± 0.24 sec for *A. alexandri*. These values are not significantly different from those measured when food was unlimited.

DISCUSSION

TERRITORIAL BEHAVIOR

Under both conditions of food availability territory owners spent large amounts of time out-of-sight (Table 1). Because *L. clemenciae* established territorial perches in thick riparian habitat it is likely that during most of the OOS time the territory owner was actually perched. Territory owners usually went OOS during a chase and could easily be missed returning to a perch high in a tree. Often birds recorded as being OOS were detected when they began to call or sing. Thus, we have likely underestimated perching time in this study. A large amount of perching time, about 80% of the total activity budget, is characteristic of other hummingbirds that have been studied (e.g., Stiles 1971).

Perches used by territory owners varied frequently, even within a single day. No preference was shown for perches near the territorial feeder (within 5 m). Territory owners sang or called regularly during each hour of observation while perching (see Kuban and Neill 1980, Powers and Conley 1994). During our observation periods we could hear adjacent territory owners calling or singing simultaneously with the territory owner being observed. Kuban and Neill (1980) suggested that the close proximity of calling *L. clemenciae* males along with their complex aggressive behaviors might indicate lekking behavior. The possibility of lek behavior, or some other structured social system, is certainly supported by the strong participation of territorial males in aggressive interactions with conspecifics regardless of energy availability (see below). Fly-catching and chase activity most often originated from a territorial perch. These activities, although significant to the territory owner, made up only a fraction of an hourly time budget (Table 1).

ENERGY INTAKE

Over the long-term hummingbirds, like any other animal, must consume an amount of food sufficient to meet their daily energy needs. Although measurements of food consumption (energy intake) are at best only rough estimates of FMR, they can be compared with more direct

measures of daily energy expenditure to assess energetic success. When food was unlimited *L. clemenciae* territory owners consumed 114 kJ/day, 39% more than their FMR measured with doubly labeled water (82 kJ/day when food is unlimited; Powers and Conley 1994). It appears therefore that *L. clemenciae* had no difficulty meeting its energetic needs assuming FMR was not substantially greater than 82 kJ/day. Yet, because most aspects of the environment are subject to change from year-to-year, it is possible that the higher energy intake indicates that FMR in this study was higher than that measured by Powers and Conley (1994). Obvious factors that can affect FMR are the thermal environment and differences in activity. Maximum and minimum T_e reported by Powers and Conley during their FMR measurements were 34°C and 15°C, respectively. Although average maximum daytime T_e in this study was the same as that reported by Powers and Conley, average minimum nighttime T_e was 6°C cooler. If we assume that this 6°C temperature difference was maintained throughout the night, then FMR would be increased by only 3 kJ (assuming thermal conductance is 0.04 kJ hr⁻¹°C⁻¹; Lasiewski and Lasiewski 1967). It is therefore unlikely that differences in the thermal environment caused FMR to be substantially different from that reported by Powers and Conley. No time budgets were conducted during Powers and Conley's FMR measurements so it is impossible to determine if a difference in activity level contributed to the high energy intake observed in this study. However, food consumption in this study did not differ significantly from measurements made under similar conditions by Powers and Conley (1994) suggesting that energy requirements for territory owners in these two seasons were comparable.

The feeding pattern exhibited when food is unlimited differed from that observed in other free-living hummingbirds. For example, Anna's Hummingbirds (*Calypte anna*) and Broad-tailed Hummingbirds (*Selasphorus platycercus*) exhibit a bimodal feeding pattern which includes a peak in feeding activity prior to roosting (Wheeler 1980, Calder et al. 1990). Calder et al. (1990) suggest that this feeding pattern is employed by hummingbirds to delay the increased cost of flight activities that would result from mass gain associated with the consumption of large volumes of nectar. However, in this study feeding rate (visits/hr) is relatively constant all day for both

L. clemenciae and *A. alexandri* (Fig. 1), and energy intake (kJ) declined continually, reaching its lowest point just prior to the onset of the nocturnal fast (Fig. 2). Because daytime mass changes of birds in this study were not monitored (e.g., Calder et al. 1990), we can only speculate as to the reasons for this difference in foraging patterns. One possibility is that if the cost of foraging is low when food is unlimited, then birds that synthesize the bulk of their fat in the morning rather than in the evening might not be in danger of experiencing a net energy deficit. This is mildly supported by the fact that mass measurements made throughout the day on *L. clemenciae* and *A. alexandri* when food is unlimited suggest that mass plateaus quickly in the morning and remains constant the rest of the day (Powers, unpubl. data).

INTRA-SPECIFIC COMPETITION

Assuming the FMR of *L. clemenciae* is about 82 kJ/day, then to remain in energy balance they must consume approximately an equivalent amount of energy from their food source each day. The ability of *L. clemenciae* to intake enough energy to maintain energy balance will depend on the quality of their food source and on the level of competition. In this study nearly all intra-specific interactions engaged in by territory owners involved intruding male *L. clemenciae*. On rare occasions female *L. clemenciae* did attempt to feed at territorial feeders, but such intrusions were too infrequent to assess the response of the territory owner. Our analysis therefore focuses solely on male intruders.

The unlimited food availability condition of this study presumably represents a high quality food source that is compact and easily defensible. Under this condition intrusion rate was high, averaging about 8 intruders/hr. Territory owners were able to expel 81% of these intruders. Those intruders that successfully fed at the territorial feeder usually did so while the territory owner was away on a chase. This could be done easily because intra-specific chases often last several minutes and often involve up to four *L. clemenciae*. The reasons why so many male *L. clemenciae* were sometimes involved in territorial chases is unclear. However, it is possible that (1) neighboring territory owners became involved when a chase passed through their territory, or (2) cooperation among neighboring territory

owners or intruders provides some energetic or social benefit. Intra-specific chases did appear to be more energetically expensive than inter-specific chases, at least in terms of their duration, so cooperative defense might be beneficial to all territory owners in a given area. Cooperative defense might also make sense if *L. clemenciae* does indeed form leks. Such behavioral mechanisms would probably be more important when energy is limited because when energy was unlimited intake by territory owners exceeded their estimated FMR by 39%. Meeting daily energy demands was therefore not a problem for territory owners even though numerous interactions took place.

The 114 kJ/day provided to territory owners during the food restriction experiment was presumed to represent a condition of energy limitation. This is supported by the fact that all food provided during food restriction experiments was consumed. Because this amount of energy is only 39% higher than the predicted *L. clemenciae* FMR, the territory owner would presumably have to work harder to retain 82 kJ for himself. This task was made easier for the territory owner because intra-specific intrusions decreased by 40% when energy was limited, which should result in an energy savings because there are fewer intruders to chase. This is supported by the fact that energy consumption by territory owners decreased to 64 kJ/day. This is almost 30% less than the DLW estimate of *L. clemenciae* FMR. Alternatively, territory owners might not have been able to meet their energy needs from the territorial feeders under these conditions and had to forage elsewhere during the afternoon period. Extra-territorial foraging might have contributed to the increased OOS time observed during food restriction. Even if territory owners were unable to meet their entire energy need from the territorial feeders, they still actively defended their territories in the same manner for the duration of the study. Chases that occurred were similar to chases observed when food was unlimited and, like the unlimited energy condition, the territory owners chased 80% of the total intra-specific intruders. Thus, regardless of the energy availability, territory owners worked vigorously to repel intra-specific intruders from their territories. This suggests that aggression serves purposes beyond the simple defense of a food source, which is consistent with our first hypothesis.

INTER-SPECIFIC COMPETITION

Male and female *A. alexandri* compete for many of the same food resources as *L. clemenciae* at the Southwestern Research Station in the Chiricahua Mountains. In most areas of its range, male *A. alexandri* is a successful territorial species (e.g., Ewald and Bransfield 1987). However, at our study site male *A. alexandri* behave as a non-territorial species, presumably because they are unable to displace *L. clemenciae*, a species nearly three times larger. We have no quantitative data on the ratio of male to female *A. alexandri* (not all birds were marked), but 70% of the total intrusions on *L. clemenciae* territories involved females. It is therefore likely that female *A. alexandri* are more numerous than males in our study area. We observed no discernible difference in the interactions between territory owners and intruding *A. alexandri* of different sexes, so the results of all *A. alexandri* intrusions are combined for analysis.

When food was unlimited, feeding from experimental feeders did not appear to be difficult for *A. alexandri*. Territory owners chased only 11% of the *A. alexandri* intruders so most were able to feed unmolested. The low proportion of *A. alexandri* chased is consistent with observations made by Powers and Conley (1994), where *L. clemenciae* territory owners chased only 4% of the *A. alexandri* intruders. Potential reasons for the low proportion of *A. alexandri* chased include: (1) because energy was available in an unlimited amount, *L. clemenciae* could ignore *A. alexandri* without cost, (2) *A. alexandri* often did not approach the experimental feeders until the territory owner was off the territory, thus reducing the chance of being chased, and (3) intra-specific interactions were relatively frequent and received higher priority from territory owners. Additional evidence that *A. alexandri* was able to forage relatively freely from experimental feeders when food was unlimited comes from the fact that 484 kJ/day was being removed from the feeders. This is slightly less than six times a territory owner's FMR based on DLW. Substantial amounts of sucrose solution were therefore being removed by intruders, predominantly *A. alexandri* (about 103 kJ/day) and wasps.

During the food restriction experiment the number of intruding *A. alexandri* was greatly reduced. However, territory owners chased nearly

half the *A. alexandri* that intruded on their territory (although the total number of chases did not differ between conditions). We believe this indicates that territory owners were more aware of intruding *A. alexandri*. If correct then this also supports our first hypothesis. During this phase of the study, territory owners could not count on an endless supply of sucrose solution and presumably would incur cost if *A. alexandri* were allowed to intrude unmolested as before. In addition, because the number of intra-specific interactions was substantially decreased during this experiment, territory owners would have more time to defend their feeders against inter-specific intruders. This is supported by the fact that the proportion of successful intrusions (where intruders actually fed from the feeder) decreased by 18% and the total number of successful intrusions decreased by 74%. Territory owners were successful in preventing substantial nectar loss to intruders, allowing *A. alexandri* to remove only 27 kJ/day. (Wasps were not feeding on the sucrose solution during this phase of the experiment.) This is enough energy to support only a single *A. alexandri* based on the DLW estimate of FMR (actually several *A. alexandri* got small amounts of sucrose solution). The 114 kJ/day available should therefore have been enough to meet a territory owner's energy need even if their FMR was not reduced when energy was restricted as suggested above, and assuming only a small amount of nectar loss to intra-specific intruders (intruding *L. clemenciae* on average fed for less than 1 sec/hr).

An alternative explanation for the behavioral changes that occurred when food was restricted is that the data were collected during a period when the birds were shifting from breeding to non-breeding status. The hummingbirds arrive in the Chiricahuas in late March to early April, and breed (in some cases) until mid July (see Johnsgard 1983 for discussion). During the latter portion of June (when food restriction experiments were conducted) it is possible that the birds' behavioral pattern changed naturally as our study encroached on the end of the breeding season. However, when the behavior of hummingbirds in this study during the unlimited food condition (observed in early June) is compared to that of the same hummingbird population in early July under the same experimental conditions (Powers and Conley 1994), no discernible difference is

observed. In addition, other studies involving these hummingbird populations (Pimm 1978, Pimm et al. 1985) report data collected between April and June, and do not identify behavioral shifts attributable to seasonal change. We therefore feel that it is unlikely that the time of measurement in this study affect our behavioral data, and that the changes observed were due solely to experimental manipulation.

CONCLUSIONS

This study illustrates behavioral changes that occur in territorial *L. clemenciae* in response to changes in food availability. When food availability is high *L. clemenciae* appears to focus on social interaction with conspecifics, while ignoring frequent visits by inter-specific intruders (*A. alexandri*) that can remove large amounts of food from the territorial food source. *Lampornis clemenciae* does not seriously exclude *A. alexandri* until food becomes limited. This suggests aggression towards intra-specific and inter-specific intruders is initiated based on different primary factors. Inter-specific aggression appears motivated primarily by food availability. If *L. clemenciae* habitat has a rich supply of food then overall hummingbird diversity is likely to be high because other species will have access to food sources, even if they are being defended.

Although food availability certainly plays a role in initiating aggression against conspecific intruders, social factors are likely just as important. Territory owners exhibited strong aggression against conspecific intruders under all conditions of food availability. The only aspect of this aggression that was clearly related to changes in food availability was frequency of occurrence. It makes sense that when food availability is low that even *L. clemenciae* density will be decreased. However, the characteristics of aggressive interactions between territory owners and intruders were not obviously altered when food availability was changed. Thus, the territorial behavior exhibited by *L. clemenciae* possibly serves a function beyond the simple defense of a food source (hypothesis #1). We must, however, be cautious in our interpretations and recognize the possible alternatives. For instance, the food source used in this study was artificial. It is therefore possible that the emphasis on conspecific chases have been selected for evolutionarily by natural conditions that depart widely from artificial feeders. A second alternative results from the like-

lihood that the larger *L. clemenciae* intruders would, over the long term, consume more nectar than the smaller *A. alexandri*. For this reason alone it might be more important for territory owners to focus on inter-specific intruders.

A second conclusion from this study centers around the behavior of *A. alexandri*. *A. alexandri* typically is a territorial species. However, at our study site they were non-territorial. This suggests that the territorial nature of *A. alexandri* is not a requirement for survival. This observation brings into question the notion that territoriality, at least in *A. alexandri*, is an evolutionarily derived trait rather than one of perhaps many behavioral options that can be employed in a variety of community interactions.

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