The Effects of Resource Availability on Territorial Behavior of the Ruby-Throated Hummingbird (*Archilochus colubris)*

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Abstract

Ruby-throated Hummingbirds (*Archilochus colubris*) often migrate to their summer breeding grounds, sometimes before their main food source, nectar from flowers, becomes available. On Douglas Lake at the University of Michigan Biological Station, Pellston, MI, we explored how resource availability affected aggressive behavior in hummingbirds. Eight lakeside sites had either a single or triple set of hummingbird feeders. We predicted that the richness of a resource site would determine the number of aggressive interactions initiated by males, with the more resource-rich sites experiencing higher frequencies of male-initiated territorial behavior. We also hypothesized that males would express more territorial behavior (chases and vocalizations) than females. We counted two types of territorial behavior in both males and females: chasings and vocalizations. Our results showed that more male aggression occurred at the resource-rich triple feeder sites, but there were more instances of female aggression than male aggression, especially at single feeder sites. Resource availability of a given site seems to be a determining factor affecting the distribution of each sex.

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Ruby-throated Hummingbirds (*Archilochus colubris*) often migrate to their summer breeding grounds, sometimes before their main food source, nectar from flowers, becomes available. On Douglas Lake at the University of Michigan Biological Station, Pellston, MI, we explored how resource availability affected aggressive behavior in hummingbirds. Eight lakeside sites had either a single or triple set of hummingbird feeders. We predicted that the richness of a resource site would determine the number of aggressive interactions initiated by males, with the more resource-rich sites experiencing higher frequencies of male-initiated territorial behavior. We also hypothesized that males would express more territorial behavior (chases and vocalizations) than females. We counted two types of territorial behavior in both males and females: chasings and vocalizations. Our results showed that more male aggression occurred at the resource-rich triple feeder sites, but there were more instances of female aggression than male aggression, especially at single feeder sites. Resource availability of a given site seems to be a determining factor affecting the distribution of each sex.

Introduction

The distribution of birds is affected by the availability and distribution of their resources (MacArthur and MacArthur 1961; Wilson 1974; Cody 1985). We investigated one aspect of resource availability, the effect of different concentrations of food resources, on the behavioral interactions of male and female Ruby-throated Hummingbirds (*Archilochus colubris*) shortly after their arrival on the breeding grounds when resources are likely to be in relatively short supply.

Ruby-throated Hummingbirds have been recorded to arrive in New Brunswick, Canada by mid-May (Christie 1980), which is at the same approximate latitude as the the University of Michigan Biological Station. When they first arrive to these northern breeding grounds in the spring, the hummingbirds' nectar resources are scarce, as their peak northern movement does not coincide with the flowering of any particular plant species (Bertin 1982). Often, sap wells created by the Yellow-bellied Sapsucker (*Sphyrapicus varius*) serve as a source of food when nectar is scarce, and therefore affect the timing of the hummingbird's arrival (Miller and Nero 1983).

Ruby-throated Hummingbirds are a good species to test effects of food scarcity because of their dependence on local food resources (especially soon after arriving on their breeding grounds) and their tendency to feed at feeders, which allows experimental manipulation of resource richness. At a location where the hummingbirds are one of the few avian species depending on nectar as a food source, and that hover to access food. Males in most bird species tend to exhibit more aggressive behavior during breeding seasons, when territories are established to protect food resources and to attract mates (Tamm et al. 1989). Ruby-throated Hummingbirds are especially competitive over feeding territories; a male hummingbird will drive away any other hummingbird that approaches its territory, regardless of sex, with the exception of potential or current mates (Stiles and Wolf 1970). Male hummingbird territories have been observed to be centered around a food source (Pitelka 1942).

We predict that sites with more feeders will be positively associated with increased aggressive interactions, especially among males. We hypothesize that more male-initiated behavior will be observed at the multiple-feeder sites compared to single-feeder sites, as a result of increased competition for the richest food resource sites. Further, we predict that hummingbirds will exhibit more aggressive behavior at dawn and dusk, when energy stores are being replenished and accumulated, respectively. Because Ruby-throated Hummingbirds are polygynous, we expect that males will compete for resource-rich sites not only to obtain the best food resources, but also to attract females.

Materials and Methods

The study was conducted in a mixed deciduous/conifer forest dominated by nine tree species, including White Pine (*Pinus strobus*), Big-tooth Aspen (*Populus grandidentata),* and Northern Red Oak (*Quercus rubra)* (Curtis et al. 1997) at the University of Michigan Biological Station, Cheboygan County, Michigan. We placed feeders of approximately 250 mL at eight different sites 60 m apart, each approximately 5-10 m from the shore of Douglas Lake, the approximate diameter of Ruby-throated Hummingbird territories (Stokes and Stokes 1989). Four sites had clusters of three feeders and four sites had one feeder; they were randomly placed.

Each of the feeders was in partial shade and near cabins that were located approximately 20-25 m of most of the feeders. We hung each feeder in a white pine (*Pinus strobus*) 1.5 m from the ground and within 0.5 m of the trunk of the tree. If a site had three feeders, they were all hung on the same tree, and all were visible from the observation point. Each feeder was anchored to the ground with transparent filament fishing line, to minimize movement in the wind. To ensure that only hummingbirds visited the feeders, we removed perches below each feeding hole, so that any non-hovering bird would be unable to use the feeders.

The solution was composed of four parts water and one part sucrose. The water was boiled in order to dissolve the sucrose. We added 4 drops of red dye per gallon of solution to ensure that the general appearance of all feeders was red, because some of the containers were red and others transparent. This was to control for potential effects of the attractiveness of different colors to foraging hummingbirds (Miller and Miller 1971). We kept the feeders filled with solution throughout the duration of the study.

We monitored hummingbird behavior on 28 and 31 May, and 4 June 2014. Hummingbird activity at the feeders was recorded each day between 06:30-07:00, 11:00-11:30, 15:30-16:00, and 20:00-20:30. Weather conditions were clear (no precipitation) on all observation days. To minimize potential observer bias, we rotated observers at each feeder or cluster of feeders during each sampling period. We observed birds by sitting 3-5 m from the feeders, which was close enough to determine the sex of the birds, but far enough away to not disrupt hummingbird activity. Interactions were categorized into two main categories: chasing (one bird driving another away from the feeder) and vocalizations (a bird emitting call notes). Each observation was noted as either male- or female-initiated. Males were identified by their bright red, iridescent throat. We did not record the sex of the bird being chased. After data were collected, we used chi-squared tests to determine p-values of the differences between the frequencies of male-initiated and female-initiated behaviors, and the differences between the frequencies of interactions at single and triple feeders.

Results

Differences in Interaction Frequency Between Sexes

Female-initiated interaction events (N=1047) were found to occur at a higher frequency than male-initiated events (N=854) (Fig. 1). This applies to both chasing and vocalization events, although the differences in frequency of male and female events were not statistically significant. More male-initiated interactions were observed at triple feeder sites (N=783), while more female-initiated interactions were observed at single feeder sites (N=974); this difference was found to be statistically significant (X^2=372.32, $P < 0.0001$) (Fig. 1).

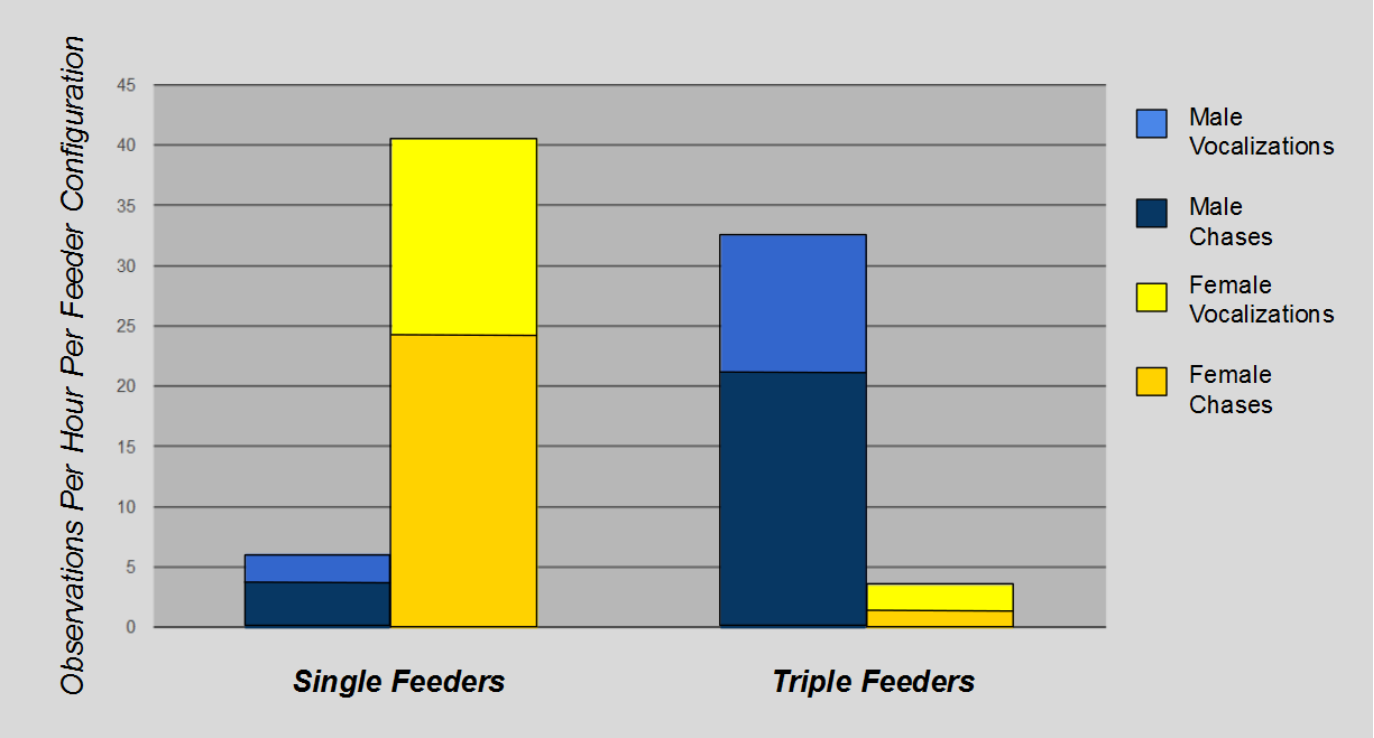

Fig. 1: Average overall interactions per hour per feeder configuration over entire observation period (28 May - 4 June 2014).

Differences of Interaction Events Throughout the Day

At triple-feeder sites, the highest number of interactions occurred at the 06:30 observation periods (N=275), then dropped gradually over the later time periods, culminating with the lowest frequency of interactions at the 20:00 observation period (N=173) (Fig. 2).

At single-feeder sites, the number of interactions started out lower than the number of interactions at triple-feeder sites at 06:30 (N=244), but gradually increased throughout the day. The highest level of interaction occurred at the 15:30 observation period (N=330) before dropping again at 20:00 (N=243) to approximately the same levels of interactions that were observed at 06:30 (Fig. 2). When summed, the average of the total observed interactions (male- and female-initiated) remained constant from 06:30 to 11:00 (N=519), peaked at 15:30 (N=542), then dropped at 20:00 (N=416) (Fig. 2).

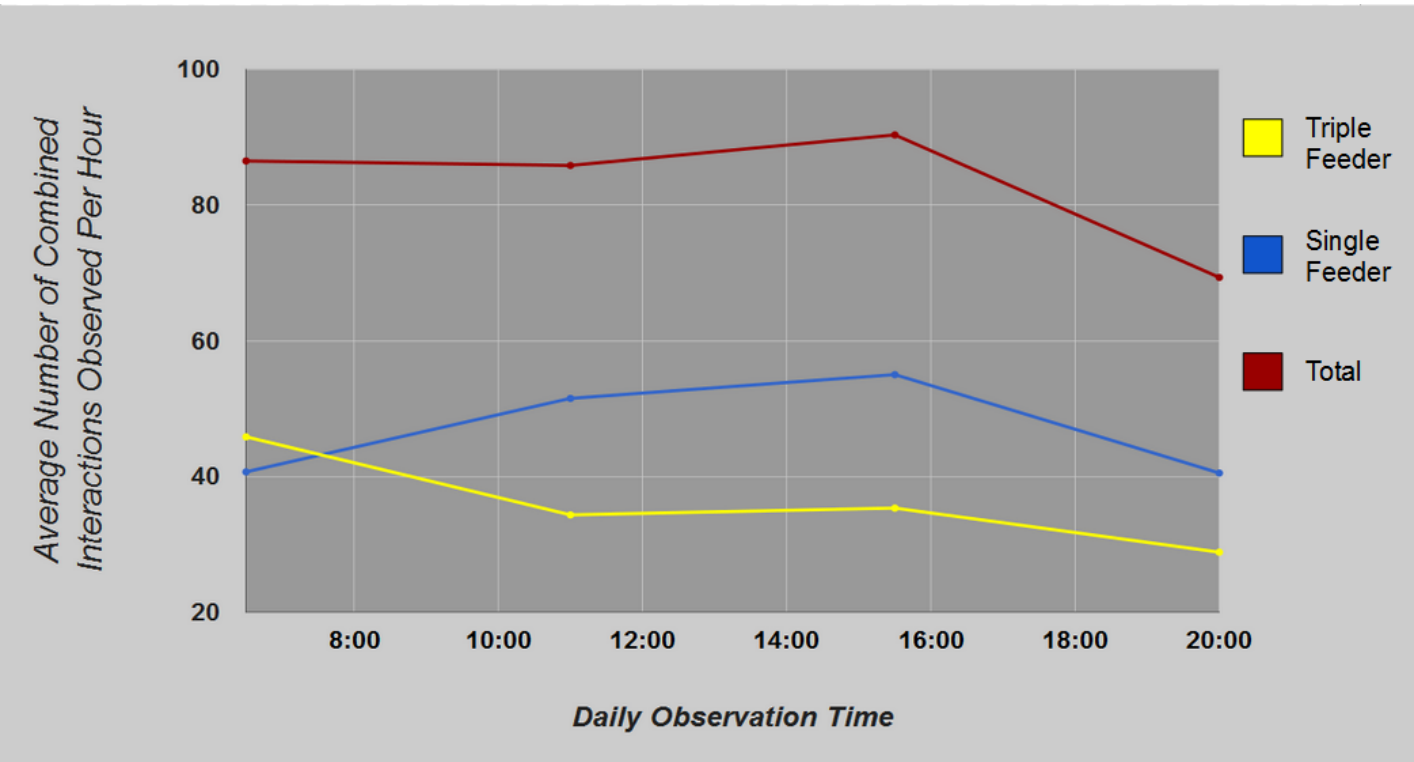

Fig. 2: Average interactions per hour throughout the day, comparing changes in total interactions at both types of feeding sites.

Differences of Interaction Events Throughout Study Period

The frequency of both male-initiated and female-initiated interactions decreased from the first day of observation 28 May, to the last day of observation 4 June (Fig. 3). The overall trend of total interactions also reflected the same decline as observed in the individual trends of interactions of both sexes (Fig. 3). On 4 June, we noticed many short foraging visits made to the feeders, with a considerable decline in aggressive interactions.

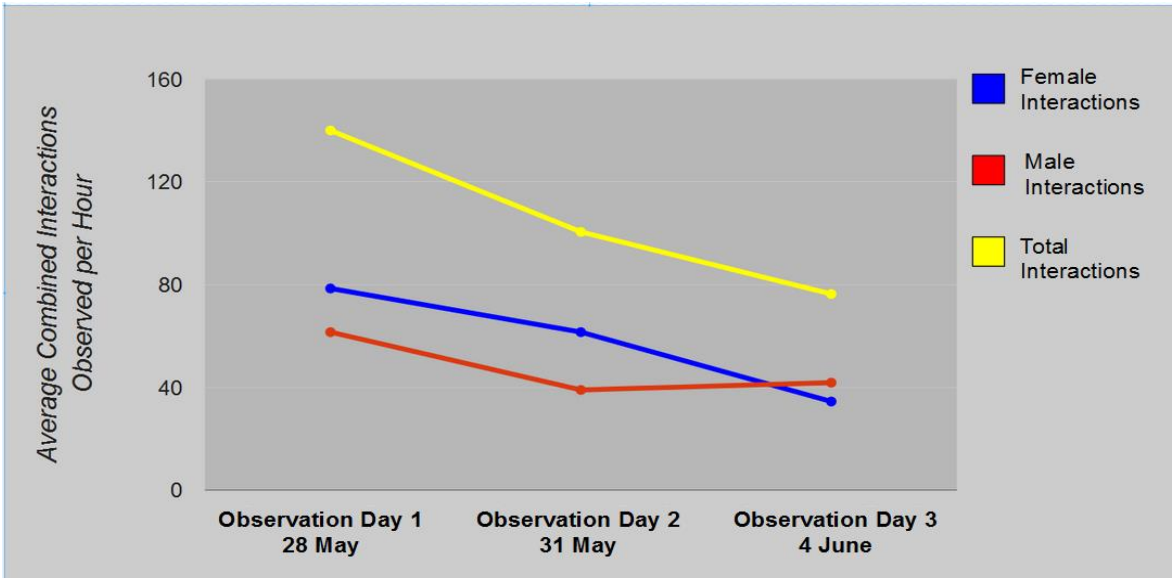

Fig. 3: Average interactions throughout observation period, examining the change in frequencies of male-initiated and female-initiated interactions over the entire observation period (28 May - 4 June 2014).

Qualitative Behavioral Observations

One hummingbird behavior that was observed in high frequency (in both sexes) was perching on a branch in close proximity to the feeders, often accompanied with quick, small head movements. The birds that were observed carrying out this "guarding" behavior usually also vocalized and/or chased any other hummingbirds that came into the site and attempted to feed. Usually, one hummingbird dominated a site over a time period, but may not have retained dominance throughout half-hour observation periods. On rare accounts, simultaneous feeding was observed among females, during which multiple times females used the same feeding site concurrently without demonstrating any aggressive behavior. Simultaneous feeding was never observed among males.

Several instances of courtship display were recorded at feeder sites throughout the study. In the courtship display, the male hummingbird performs a dive display consisting of a U-shaped looping dive starting from as high as 12–15 m above the female; once the female perches, the male hummingbird display shifts to a series of extremely fast, very close, side-to-side horizontal arcs (Fig. 4: Shuttle Display), with gorget extended, performed within 0.5 m of female (Robinson, et al. 2013). Over the course of the study, we observed 20 courtship displays. A total of 14 courtship displays occurred at triple-feeder sites. Both sites with the highest cumulative frequencies of courtship displays (6 displays and 5 displays, respectively) were observed at triple-feeder sites.

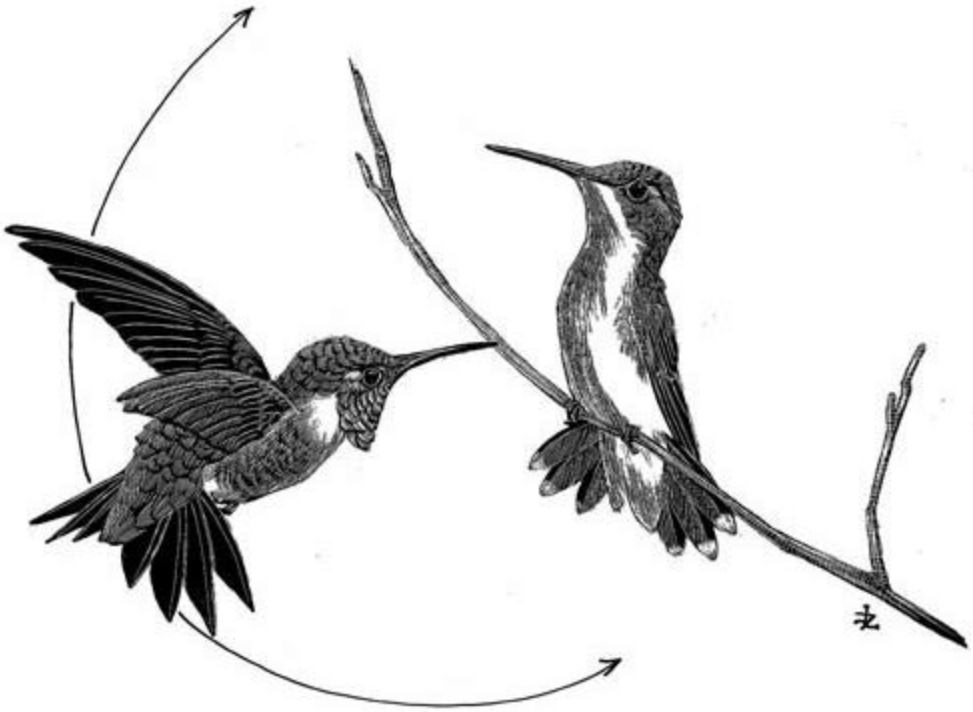

Fig. 4: Male Ruby-throated Hummingbird Shuttle Display towards female; Drawing by J. Zickefoose from Birds of North America Ruby-throated Hummingbird Account (2013).

Though we removed the perching posts from every feeder with the intention of only providing access to hover-feeders, we witnessed two other species successful feeding from feeders. During the 06:30 observation period on 4 June, a Baltimore Oriole (*Icterus galbula*) landed on the fishing wire suspending one of the three feeders at a triple feeder site. It perched on the line while feeding from the hummingbird sugar solution, without damaging the feeder. There were no hummingbirds present at the time of this event. The Baltimore Oriole fed and left without any apparent disruption to the site.

On the same day during the same observation period, a Yellow-bellied Sapsucker (*Sphyrapicus varius*) attempted to land on a single feeder. However, the lack of post on the feeder prevented it from doing so, and it left the feeder. The bird did not appear to cause any disruption of hummingbird feeding activity, and had no interactions with any hummingbirds. During the 08:30 observation period on 4 June, another, if not the same, Yellow-bellied Sapsucker was observed successfully landing on a feeder at another triple feeder site. Clinging with his legs to the bottom rim of the feeder, the Yellow-bellied Sapsucker was able to access the sugar solution, and proceeded to land on the adjacent feeder in the same site, and fed again. A male Ruby-throated Hummingbird began feeding as the Yellow-bellied Sapsucker continued, but no interaction between them occurred, and the Yellow-bellied Sapsucker flew away after his second consecutive feeding.

Discussion

We expected that at both single and triple feeders, there would be a greater number of aggressive behaviors initiated by males than by females, and additionally predicted that the total number of male interactions would be greater at triple feeder sites than male interactions at the single feeder sites. This prediction was based on the assumption that males of most bird species tend to exhibit more aggressive

behavior than females (Tamm et al. 1989). We also hypothesized that aggressive behavior would increase along with competition at the most resource-rich sites (triple feeders).

Although we observed that the majority of aggressive interactions were initiated by male hummingbirds at the triple feeder sites, single sites had more female-initiated interactions (Fig. 1). The average number of female-initiated interactions per site per hour at the single feeders was also greater than the number of male-initiated interactions per site per hour at the triple feeders (Fig. 1). Our results suggest that males concentrate on defense of the richest food sources. The occurrence of the majority of courtship displays at triple feeder sites, where there was also the most male territorial behavior, suggests that one driver for male territoriality in our study was the attraction of mates.

Though males were aggressive at single feeder sites, they appeared to preferentially select the more resource-rich (triple feeder) sites. As a result, females may have been relegated to the single feeders, which they used more frequently and consistently. Although males occurred disproportionately at the more resource-rich sites, they did not necessarily exhibit a higher quantity of aggressive acts. Males and females differed in which sites they aggressively defended, but both sexes initiated vocalizations and chases. Based on these results, resource richness may be a significant determining factor of distribution of males and females, yet both sexes exhibit aggressive interactions at feeding sites.

We originally predicted that territorial behavior would occur at higher levels at 20:00 and 06:30 in order to store and replenish reserves needed for the night. However, our observations demonstrated an overall increase in total aggressive behavior during the middle of the day (especially at 15:30) as opposed to early morning and evening observations (Fig. 2). Similar results were found in a study involving Cinnamon Hummingbirds (*Amazilia rutila*), Steely-vented Hummingbirds (*Amazilia saucerottei*), and Scaly-breasted Hummingbirds (*Phaeochroa cuvierii*), in which feeding behavior and chases were recorded at the site of a flowering tree (Stiles and Wolf 1970). Although feeding activity was found to be most frequent in the early morning and evening, and lower during the middle of the day, the number of chases per minute tended to be lower in the morning and evening, peaking in the middle of the day (Stiles and Wolf 1970).

The results (Stiles and Wolf 1970) were consistent with the frequency of chases we observed in the Ruby-throated Hummingbirds in our study. The inverse relationship between feeding activity and chasing likely occurred because the energy expenditure required to defend and maintain a territory was too high during the high-demand time periods of dawn and dusk to be profitable (Stiles and Wolf 1970). Instead, short foraging visits were made in order to acquire sufficient energy during these times, an observation we made in our study as well. During the middle of the day, when feeding frequency is lower, the energy required to defend a territory (perform chases and/or vocalize) is profitable because there is less feeding occurring.

The total number of interactions steadily declined between the 28 May and 4 June (Fig. 3). On the last day of observation, we noted that there were markedly fewer visits to feeder sites—as well as fewer competitive interactions between birds—than observed earlier. We speculate that on 28 May, Ruby-throated Hummingbirds were arriving from their winter territories when nectar sources were scarce due to a late spring in which phenological development was delayed. The cooler spring may have delayed the blooming of flowers that might normally provide food for arriving Ruby-throated Hummingbirds. By 4 June, our final observation day, phenological development had advanced. Though we did not quantitatively measure phenology during the experimental period, it is possible that resources provided by feeders were less important to the Ruby-throated Hummingbirds' diet at the end of the observation period.

Areas of future research may include examining the sexes of the recipients of aggressive behavior in the hummingbirds; since we were unable to record the sexes of the birds being chased or vocalized at, there may have been patterns that we were unable to detect. Studies can also be done on changes in behavior throughout a longer time period, in order to examine potential differences in territoriality during other periods of the breeding season, or as resource availability changes. Individual birds could also be banded in order to ascertain if certain male hummingbirds are defending territories for extended periods during the breeding season. Our study could also be repeated in different habitats occupied by hummingbirds, to examine how aggressive behavior is affected by the presence of different sources of food in different environments.

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