Resource defense and territorial behavior of male and female Ruby-Throated Hummingbirds (*Archilochus colubris*)

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EEB 330, Biology of Birds
6/18/2015
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Abstract

Ruby-throated Hummingbirds (*Archilochus colubris*) defend a territory based on the availability of their food source. Male hummingbirds are known to be more aggressive than females as they chase away any intruders near their territory, while females have been reported to share a territory and their food source in addition to exhibiting aggressive behavior at food resources. We explored how the sex of the defending hummingbird and the amount of resources in their territory affected hummingbird aggression. We predicted that male hummingbirds would chase both male and female hummingbirds equally, whereas female hummingbirds would chase away more males than females. We also predicted that the most aggression would take place at our intermediate- resource sites because these represent the best tradeoff between resource benefits and energetic costs of defense (Rousseu et al. 2014). Results showed that intermediate-resource sites had more male-female chases while low and high resource levels were associated with more female- female chases. We also found that the most aggressive behavior occurred at low-resource sites.

Introduction

Many bird species establish a territory to secure defendable resources (Orians and Willson 1964). Ruby-throated Hummingbirds *(Archilochus colubris)* will choose a territory based on the availability of food sources, which they defend by chasing away intruders that would use the resources they control (Pitelka 1942). When hummingbirds migrate north to northern Michigan in May, they arrive before most nectar-producing flowers bloom (Miller and Nero 1983). As a result of this temporary scarcity, finding and defending a territory with suitable resources is crucial to the survival of the hummingbirds during their first weeks on the breeding ground.

Male hummingbirds are known to be particularly aggressive and will chase any intruders which threaten their food resources, occasionally chasing nectar-eating insects as well as other hummingbirds (Pitelka 1942; Stiles and Wolf 1970). Females also show aggression, but female hummingbirds have been reported to share a territory and its resources (Biswas et al. 2014).

The goal of this study was to describe any differences in the targets of hummingbird aggression depending on the sex of the defending hummingbird and the amount of resources in their territory. Rousseu et al. (2014) found that the highest levels of competition between hummingbirds occurred at sites with intermediate levels of abundance, because the lowest levels of resources were not worth defending and the sites with abundant resources took too much energy to defend relative to the benefits gained. Therefore we predicted that the most aggression would take place at our intermediate feeders. We also predicted that male hummingbirds would chase both male and female hummingbirds equally whereas female hummingbirds would chase away male hummingbirds with a higher frequency than other females.

Materials and Methods

We conducted our experiment at the edges of an open, circular field surrounded by mixed hardwood forest at the University of Michigan Biological Station near Pellston, Emmet County, Michigan. Six hummingbird feeding stations were randomly placed around the edge of the field with at least 50m separating each station, approximately the size of a Ruby-throated hummingbird's territory (Stokes and Stokes 1989) (Fig. 1). Two stations had one feeder (low resource abundance), two had two feeders (intermediate resource abundance), and two had four feeders (high resource abundance). The feeders were placed away from potential perches, so that the non-hovering animals could not reach them. Each of the feeders was filled with a solution of four parts water and one part sugar. Feeders were cleaned and the sugar water was replaced every three days. Some of the feeders were tinted red, and others were clear. Because hummingbirds are known to be attracted to the color red, we wrapped the clear feeders in red cling wrap to control for color preference. The feeders were hung between one and two meters off the ground in White Pine (*Pinus strobus*) trees.

We collected data on 30 May and 3, 6, 7, and 10 June, 2015. Since the effects of inclement weather on hummingbird feeding and chasing dynamics is unclear, we did not collect data during heavy rain or thunderstorms. On each observation day, sites were

watched at 06:30, 11:00, and 17:00 EDT. Each observation period lasted one hour. To avoid observer bias, observers were rotated to a different station each observation period. During the observation periods, one observer was stationed at each feeding site, with the exception of the high-resource sites, which had two observers in order to have clear views of all four feeders more easily. Observers maintained a distance of approximately five meters from the feeders. An activity log was kept for each feeding site, counting the number of male and female Ruby-throated Hummingbird visits as well as the sex of the target and aggressor in each chasing interaction. The sex was determined by the color of the bird's throat: red in males, white in females. Because the target of aggressive vocalizations is difficult to determine, this study focused only on chases. Additional qualitative observations such as courtship displays, apparent feeder guarding, and other species of animals interacting with the feeders and hummingbirds were also recorded.

We analyzed our data with chi-square tests to determine p-values of the difference between male and female chasing at each of the three resource levels, as well as the difference between numbers of males and females present in our study area. We also used three large-sample z-tests to generate a p-value for the difference between the amounts of aggressive behavior at each resource level.

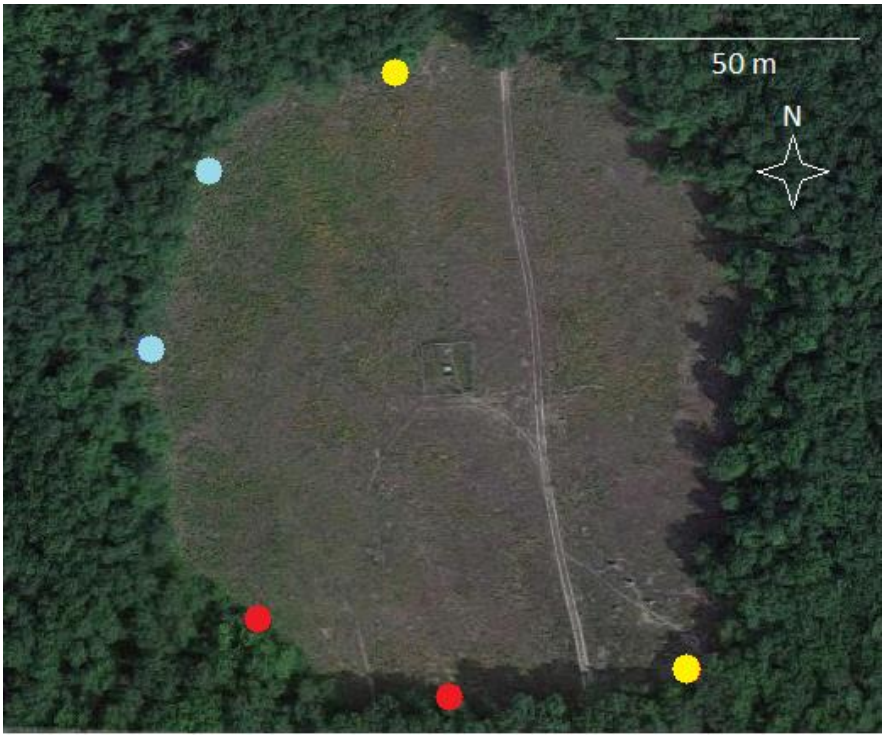

Figure 1: Approximate locations of feeding stations. Low-resource stations are red, intermediate-resource are yellow, high-resource are blue. *Source: Google Maps*

Results

Quantitative

There was a relationship between the sex-chasing scenarios (male-male, female-female, male-female, female-male) and the resource abundance levels (X^2_6=18.163, p<.01). Furthermore, female-female chases were most prevalent at low (χ^2_3= 35.96, p<.01) and high (χ^2_3=11.47, p<.01) resource abundance levels. However, intermediate sites were associated with higher frequencies of male-female chases (χ^2_3 =11.923, p<.01). The high number of male-initiated chases at intermediate sites appeared to be driven by site one (two feeders), where a male bird exhibited territorial behavior with consistent male-female chases (N=6). Only male-female chases were observed at this site.

The mean chases/hr varied among the three treatments. There were 1.04 chases/hr at low-resource, 0.54 chases/hr at intermediate-resource, and 0.71 at high-resource sites. However, this difference was not statistically significant ($F_{2,69}$= 0.926, p= 0.401). Another measure of aggressive behavior is the proportion of chases to visits (chases/visit) at each site. At low-resource sites, there were 0.2066 chases/visit, while there were 0.073 and 0.0863 chases/visit at intermediate- and high-resource sites, respectively. A series of three large-sample z-tests (with sample sizes of N=121, N=178, and N=197) compared these three chases/visit proportions by abundance levels. Due to the multiple hypotheses being tested to reach a conclusion, the Bonferroni correction was applied to the data to avoid the higher possibility of committing a type I error. The tests showed that the proportion of chases per visit at intermediate and high resource abundance sites were not significantly different (z = -.4733, p=.319). However, the proportion at low resource abundance sites was significantly higher than those of the intermediate (z = 3.4082, p < .01) and high (z = 3.0767, p < .01) resource abundance sites, even when accounting for the lower significance level (α=.0167) determined by the Bonferroni correction. Therefore, low-resource sites hosted a significantly higher level of aggressive behavior than either intermediate or high-resource sites.

Females, with 315 visits, were more common at the feeders than males, who visited 181 times. As a result, female-initiated chases were more frequent than male-initiated chases (X^2_1=9.6182, p<.01) as well as chases targeting females (X^2_1=27.6546, p<.01).

Qualitative

One instance of two hummingbirds, two females, feeding at the same time was recorded at site three (one feeder). This was the only instance of two hummingbirds using a resource site concurrently and not interacting in some way.

No other birds were observed interacting with the feeders but insects were reported to land on the feeders and drink from them. One butterfly, one dragonfly, and nine bees were seen at feeders at various observation periods. The majority of the time no hummingbirds were present while the insects were at the feeders, but there was one instance of a bee feeding at station six (intermediate resources) and a female hummingbird chasing it away.

Discussion

Our results show that significantly more aggressive behavior, as measured by chases per visit, occurred at low-resource sites than either intermediate or high resource sites, contrary to our hypothesis. The configuration of the feeders may partially explain this relationship. Single-feeder sites may bring hummingbirds in such close proximity that chases ensue more often than two and four feeder stations where available resources are more dispersed. The single-feeder sites also appeared to be female dominated, and most of the chasing seen at them involved two females or a female chasing a male (Figure 3). Females were more abundant than males at all of the feeding stations, but were the most active at the single-feeder stations compared to males. The two-feeder stations were mostly dominated by males, and the four-feeder stations had no clear dominance, which may have resulted in females concentrating at single feeder sites. Because there were so many more females than males, the activity levels were higher as well.

We further found that intermediate-resource sites had a large number male-initiated chases compared to low and high resource sites. A potential explanation for this difference is the relative abundance of females compared to males in our study combined with the greater aggressiveness of males. Biswas et al. (2014) found more females present at lower-resource sites because they were driven away from high-resource sites by more aggressive males. Therefore, males may have been unable to defend sites with four feeders, leaving them to be fought over by more abundant females and choosing instead to defend territories centering on intermediate-resource sites. This situation would leave low-resource sites to be defended by females.

Male territoriality is a possible reason for the relative scarcity of males in our study. Pitelka (1942) suggests that males are less mobile during the breeding season after they have established a territory. Males tied to their territory are thus less likely to explore the landscape for additional food sources such as our feeders, compared to females, who may not have specific territories. By 30 May, when we began observation, many males may have already claimed a territory because the bulk of migration to the breeding grounds had ended (Courter et al. 2013). Despite the scarcity of flowers in late May and early June in our latitude, males may have established territories centered around other feeders in the area or holes excavated by the Yellow-bellied Sapsucker (*Sphyrapicus varius*), where hummingbirds are known to feed (Freer 1935). Hummingbirds were in fact observed at sapsucker holes near the study site, though sexes were not noted.

Because of the lack of males, we observed a disproportionate amount of female activity and interactions involving two females. Though female hummingbird aggression is not as well documented as male aggression, it is clear from our results that females do engage in aggressive behavior. Apart from chasing, females were often observed perching near a feeder for several minutes after feeding. It is unclear whether this behavior was a way of guarding the feeder, but when one hummingbird attempted to feed while a female was perched, it was chased off. This perching behavior was not observed in males. One female went so far as to defend a feeder (site 6) from a bee. However, because the relative scarcity of male hummingbirds skewed the chasing data, we could not accurately compare the frequency of aggression based on sex (Figure 2).

Both sexes chased females more than males, but this difference may be a result of the greater number of females rather than any preferential chasing. Ultimately, we were unable to reject the null hypothesis that both sexes chase all other hummingbirds equally because of the female-skewed sex ratio.

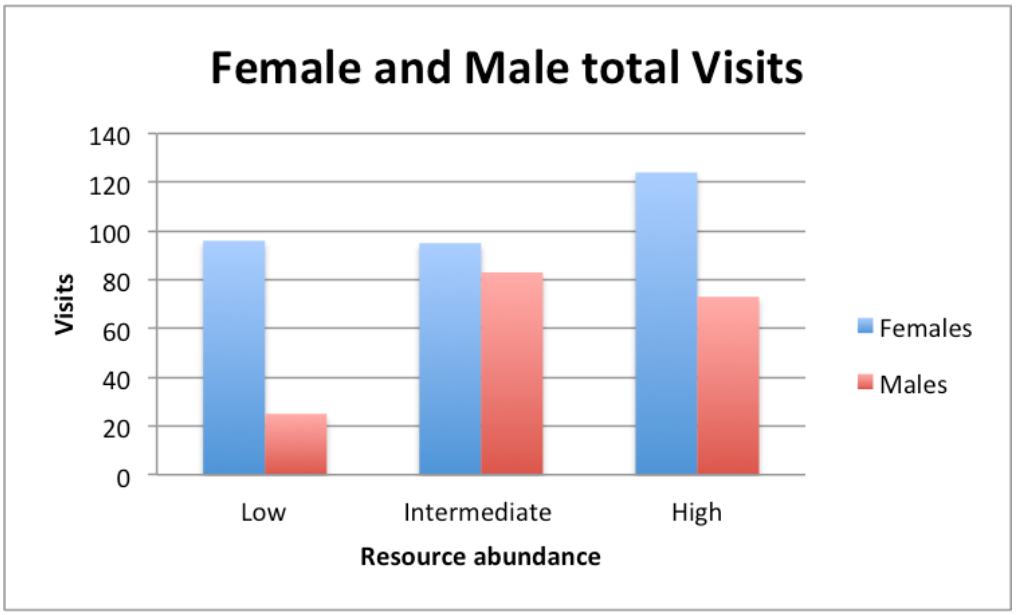

Figure 2. Female and male visits at each feeder type

The six feeding stations demonstrated a wide range of hummingbird interactions (Figure 3). Site one, an intermediate-resource site, appeared to be defended by a territorial male; the only chasing that occurred was male-initiated, and courting was observed. Females were observed looking around constantly while feeding and changing feeding positions at this site. This nervous feeding behavior was not observed at other sites. Low-resource site three, on the other hand, was entirely female-dominated. The 40 recorded female visits indicate that site three was a potential female territory. Males visited the feeder only four times and were chased away twice. Site four, a high-resource site, was the most active with 102 visits and hosted a wide variety of activity, including chases initiated by and targeted at both genders as well as courting behavior. There was no evidence of a dominant territorial bird, with the high resource abundance of the site allowing many individuals to benefit without an obvious hierarchy.

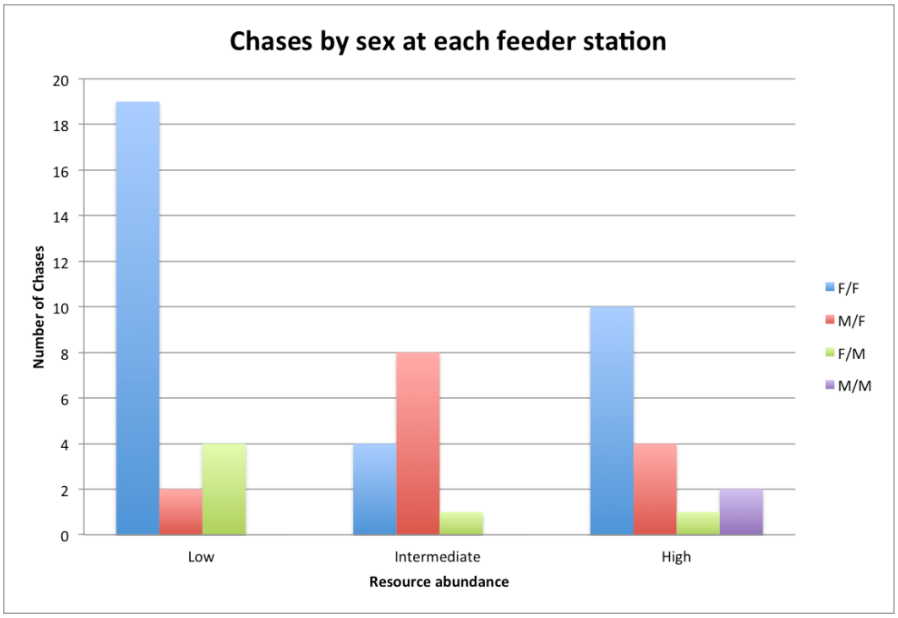

Figure 3. Chases by sex at each feeder type

Future study of hummingbird interactions would benefit from data collection during migration period as the timing of the experiment can affect the sample size and the number of interactions. For example, a similar study conducted by Biswas et al. at the University of Michigan Biological Station was able to collect a much larger sample size of interactions (N=1901) because it coincided with the weather-delayed spring migration of 2014 (D. Ewert, pers. comm. June 18, 2015). The bulk of the hummingbird migration in Michigan takes place in May. In the northern Lower Peninsula, Ruby-throated hummingbirds arrive in the last week of May; we started observing on 30 May (Wood 1951). Setting feeders up a week earlier may encourage more territories to be formed at our sites and thus alter the interactions between the birds. Additional information could have been collected by banding the birds. Banding, or some other color marking, could help us identify which individuals visit the feeder sites the most. We obtained the sex of each hummingbird that visited the feeders, but had no way to recognize individuals. Because of this we could not be sure if a specific bird held a territory or if the dominant bird changed over time. We could also get a more accurate picture of the number of hummingbirds in the population because we could then count the individuals. A similar study can also be conducted at various habitats to examine how different natural barriers and ecological system can affect competitive behavior by female and male hummingbirds.

Acknowledgements

We would like to thank Dave Ewert, Director of Conservation Science at The Nature Conservancy, and Ben Jellen, Professor of Biology at McKendree University, for their outstanding support and guidance throughout this study. We would also like to thank Nicole DesJardens, Mason Hill, Polly Washabaugh, and Laurel Wellman for their assistance in the data collection process and the University of Michigan Biological Station for their support, funding for materials, and the study site for the project.

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