

**Resource availability and territorial behavior in
Ruby-throated Hummingbirds (*Archilochus Colubris*) at
UMBS**

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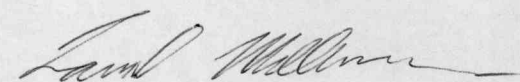
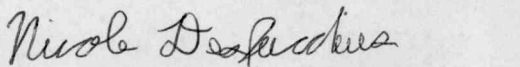
Abstract

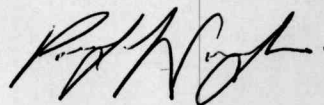

The goal of this study was to determine if Ruby-throated Hummingbirds (*Archilochus colubris*) exhibited territorial behaviors in relation to varied degrees of nectar availability. In order to examine this territorial behavior, we worked with students in the ornithology class to set-up 6 feeding sites at the edge of a field and woods at the University of Michigan Biological Station (UMBS) in Pellston, Michigan. Feeders at the sites were used to mimic low, intermediate, and high resource availability. Our group predicted that males would exhibit more territorial behavior than females at the sites with higher resource abundance. We also expected the most interactions to occur among males. We observed and recorded the territorial behavior of chasing at the feeding sites 3 times a day for hour-long periods for 4 days. Our results showed that the highest number of chasing behavior occurred at the single-feeder stations amongst females. We observed relatively low numbers of chasing between males. Furthermore, we observed that males preferred visiting sites with more feeders whereas females did not exhibit a clear preference of feeder abundance. Further studies on hummingbird territorial behavior would be beneficial to clarify whether chasing amongst females is common.

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Laurel Wellman

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Introduction

The Ruby-throated hummingbird (*Archilochus colubris*) is the only species of hummingbird that migrates from Central America to breed and spend its summers in eastern North America (Weidensaul 1996). During the migration, hummingbirds have been known to fly up to 1,000 km without stopping (Berthold 2001). They primarily inhabit lightly wooded areas and the edges of forests (Pettingill 1974). This has been linked to the hummingbird's dependence on woodlands for food (Hainsworth 1981). These birds exhibit some of the highest mass-specific rates of aerobic metabolism (215 cal/g/hr) among vertebrates (Suarez 2002). They generally spend 25% of daylight hours hover-feeding and 75% perching. This stationary time is utilized to digest food and to watch for territorial intruders (Suarez 2002). Hummingbirds obtain the majority of their dietary energy from floral nectar, although Ruby-throated hummingbirds have been documented feeding on 31 different species of plants (Suarez 2002; Johnsgard 1997). As food is a vital resource, there is great competition over feeding locations. Ruby-throated hummingbirds have been found to exhibit territorial chasing behavior in both the natural environment and in artificial feeder settings (Southwick and Southwick 1980).

Studies have found that hummingbirds are more territorial with higher resource availability (Carpenter et al. 1983). This suggests that a higher density of food is more valuable to the hummingbirds and therefore is more likely to be defended (Rousseu et al. 2014). Due to optimal foraging theory, which suggests the best foraging takes place in areas with maximum energy gain and the lowest risk of predation, hummingbirds are likely to prefer sites with higher feeder abundance (Pyke 1978). Studies suggest hummingbirds develop territories. An example study found that the hummingbirds that were concentrated in a certain area of resources and were consistent over a significant time period gained greater exclusivity at feeders (Rousseu et al.

2014). In order to maintain territories, hummingbirds limit their foraging sessions to under one minute, which increases caloric efficiency and ensures that critical fats are not burned to fuel foraging flights (Suarez 2002).

In this study, we looked at aggressive chasing behavior in Ruby-throated hummingbirds and how it differed when different amounts of resources were available. We developed two hypotheses for hummingbird behavior. We predicted a higher frequency of chasing behavior at sites with more hummingbird feeders. Additionally, we predicted that the most chasing behavior would be exhibited by males chasing other males. Our hypotheses were generated in response to a similar study performed by the Spring 2014 General Ecology class (Adams et al. 2014) along with the Spring 2014 Biology of Birds class (Biswas et al. 2014) at the University of Michigan Biological Station. These studies found that males exhibit more aggressive territorial behavior at sites with greater food resource availability. We generated our second hypothesis based on studies by Pitelka et al. which showed females generally have less of an ability to maintain territories (1942).

Materials and Methods:

Our study was conducted approximately 0.5 km south of Douglas Lake in the UV field at the UMBS (Heinen & Vande Kopple, 2003). The field is approximately 4 km². Although it contains some UMBS equipment, the field is a vacant grassland surrounded by forest. The forest consists of mainly Big-tooth Aspen (*Populus grandidentata*), White Pine (*Pinus strobus*), and Northern Red Oak (*Quercus rubra*). In collaboration with the ornithology class, we set up six feeding sites around the periphery of the field. We randomly designated a number of feeders to each site: two sites contained single feeders, two sites contained two feeders, and two sites

contained four feeders. We observed chasing behaviors at each feeding site and noted which sexes displayed and received the most aggression.

Sites were spaced approximately 50 m apart, and feeders were hung in White Pine trees approximately 2 m off the ground. Sites were spaced out in these distances to mimic the typical range of hummingbird territory. Each site bordered the periphery of the forest. At sites with multiple feeders, feeders were hung in the same tree and were visible from the field. All feeders had their perches removed to ensure that only hummingbirds would be able to visit them. In order to make the feeders consistent in coloration, we covered clear feeders with red translucent plastic wrap. We filled the feeders with a solution composed of three parts boiled, disinfected water and one part sugar. Feeders were filled approximately halfway with nectar solution. To maintain the cleanliness of the feeders, we rinsed the feeders and refilled them with solution every three days to prevent the growth of mold and fungus.

We monitored hummingbird behavior for four days in spring from late May to mid June with three observation periods a day. We initially planned for each observation period to last 30 minutes, but later extended the observation time to 60 minutes in order to increase data collection. Observations occurred at 6:30 am, 11:00 am, and 5:00 pm. Sites with one and two feeders had a designated observer, while sites with four feeders had two designated observers. Observers rotated sites in a clockwise direction between observation periods. At each site, observers recorded (1) the presence of hummingbirds and the sex present, (2) the occurrence and frequency of chasing behavior and (3) the sex of birds exhibiting chase behavior and responding to chase behavior. We used chi-square goodness of fit tests to test both of our hypotheses.

Results:

We counted the number of visits both males and females made to each feeder site and ran chi-square goodness of fit tests for each sex to determine if there was a preference for site size. For males, our results were statistically significant ($p\text{-value} < 0.0001$). While the males made only 25 visits total to the 1-feeder sites, they made 83 visits to the 2-feeder sites, and 73 visits to the 4-feeder sites. Therefore, our results suggest that males preferred to visits the sites with two and four feeders over the sites with one feeder. Our results were not statistically significant for females at the 5% level ($p\text{-value} = 0.0757$), although they do provide some evidence for preference for one type of site over another. Females made 96 visits to the 1-feeder sites, 95 visits to the 2-feeder sites, and 124 visits to the 4-feeder sites. Since the visitation count for the 4-feeder sites was higher relative to the other two, we can say that there may have been some preference for the 4-feeder sites among females. Nevertheless, the chi-squared test we used to analyze this information produced a p-value slightly above our level of significance.

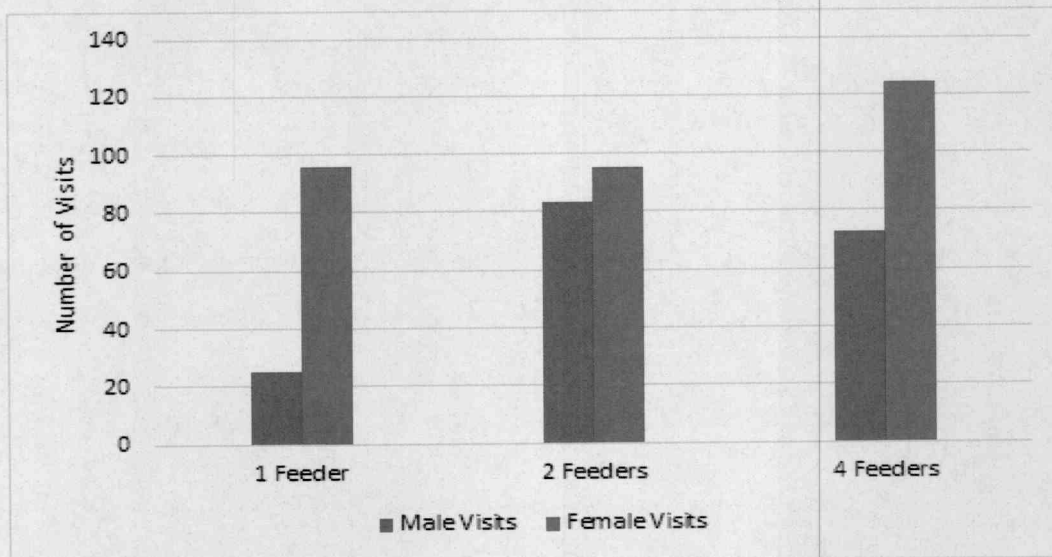


Figure 1: *Visitation at feeder sites for males and females.*

We ran a chi-squared test of independence to determine if there was a relationship between the number feeders per site and the type and amount of chasing behavior observed. It was significant at $p=0.005648$.

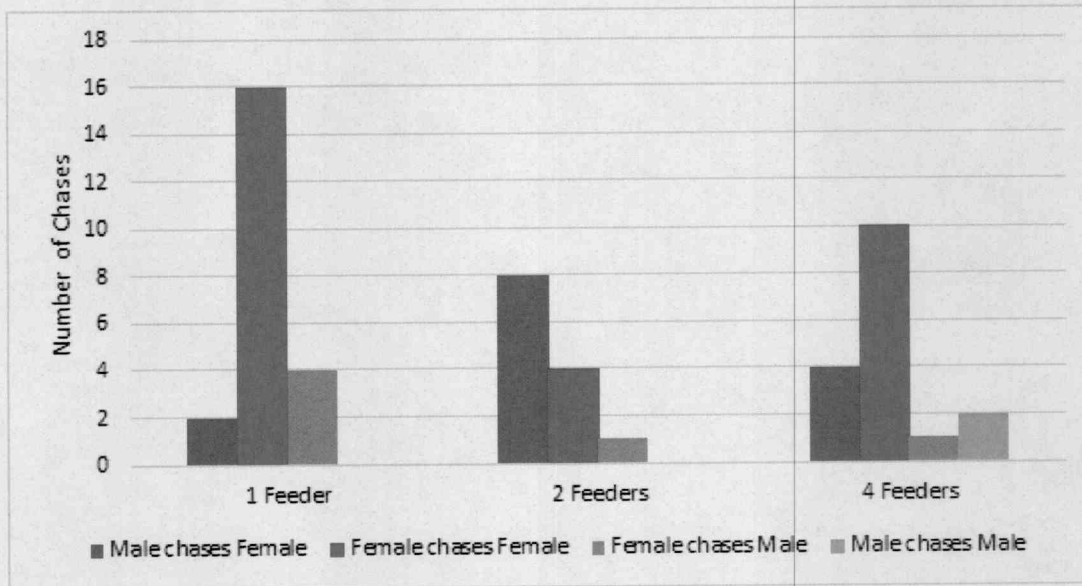


Figure 2: Types of chasing behavior observed at each type of feeder site.

To determine which aspect was significant (e.g. the sex, the number of feeders, or both) we performed a more specific chi-squared goodness of fit test on the type of chasing at all feeders combined. The results were also significant at the 5% level with a p-value of 0.00001.

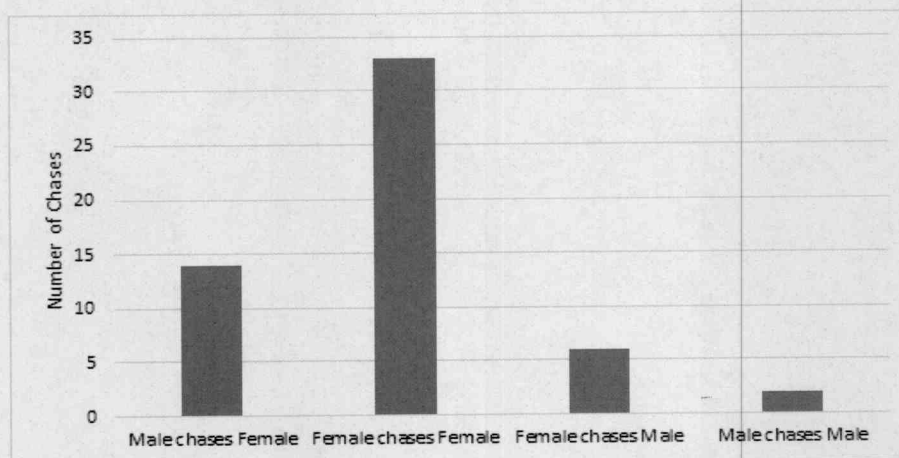


Figure 3: Amount of chasing behavior observed, categorized per type of interaction.

However, upon performing a chi-squared goodness of fit test on all chasing behavior at the different sites, we found a p-value was 0.309, which is not significant at the 5% level.

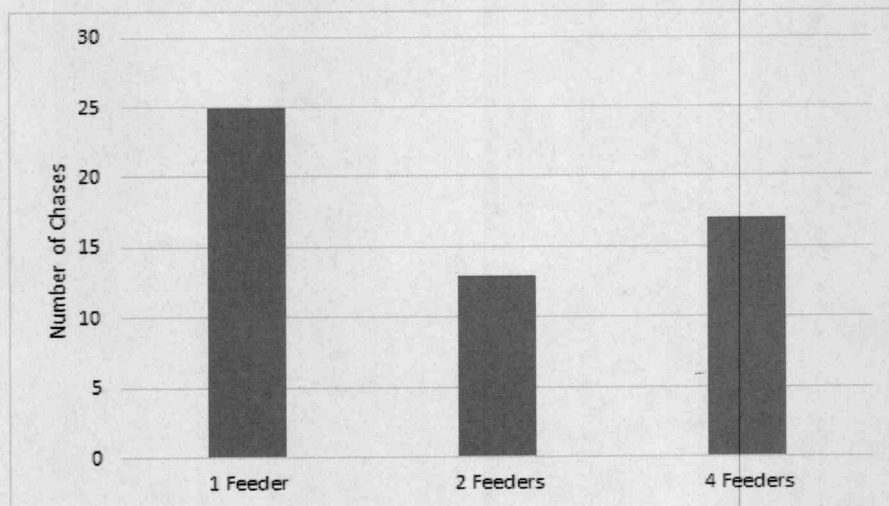


Figure 4: Amount of chasing behavior observed, categorized per type of feeding site.

Because the amount of female-female chases was the greatest, we ran a chi-squared goodness of fit test to determine if the female-female chases were more plentiful at one feeder site. Our p-value was 0.027, which is significant at the 5% level. The number of chases was the highest at the single feeder sites and lowest at the intermediate (2 feeder) sites.

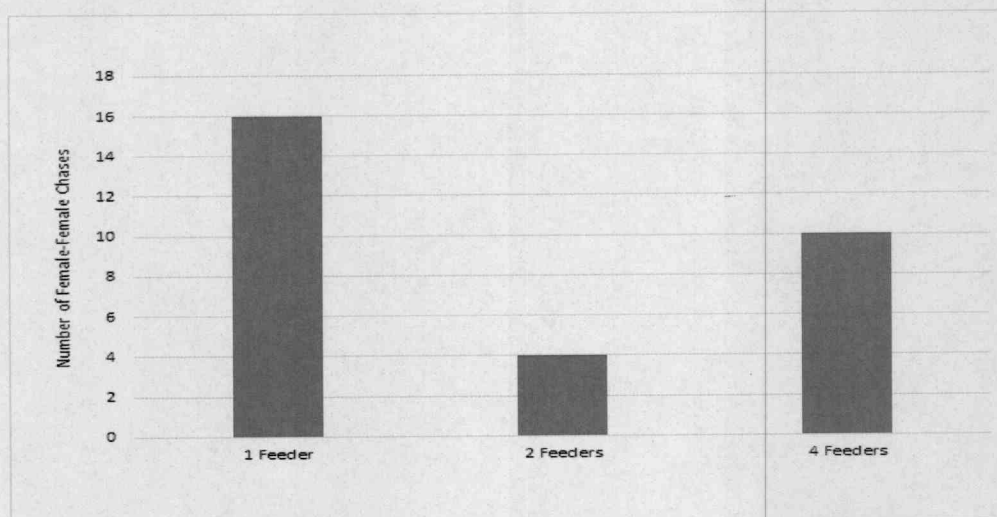


Figure 5: Number of female-female chases observed, categorized by type of feeding site.

We also performed a chi-squared goodness of fit test on the second most abundant type of chasing (male chasing female). However, the results were not significant at the 5% level (p-value=0.1003).

We noticed a potential negative correlation between the number of female-female chases and the number of male-female chases. While we cannot say for sure that there is a true correlation due to the lack of significance of the male-female chases, the totals indicate a correlation in chasing behavior. At the single feeder sites, the female-female chases were the highest while the male-female chases were the lowest. Similarly, at the 2-feeder sites the female-female chases were the lowest while the male-female chases were the highest.

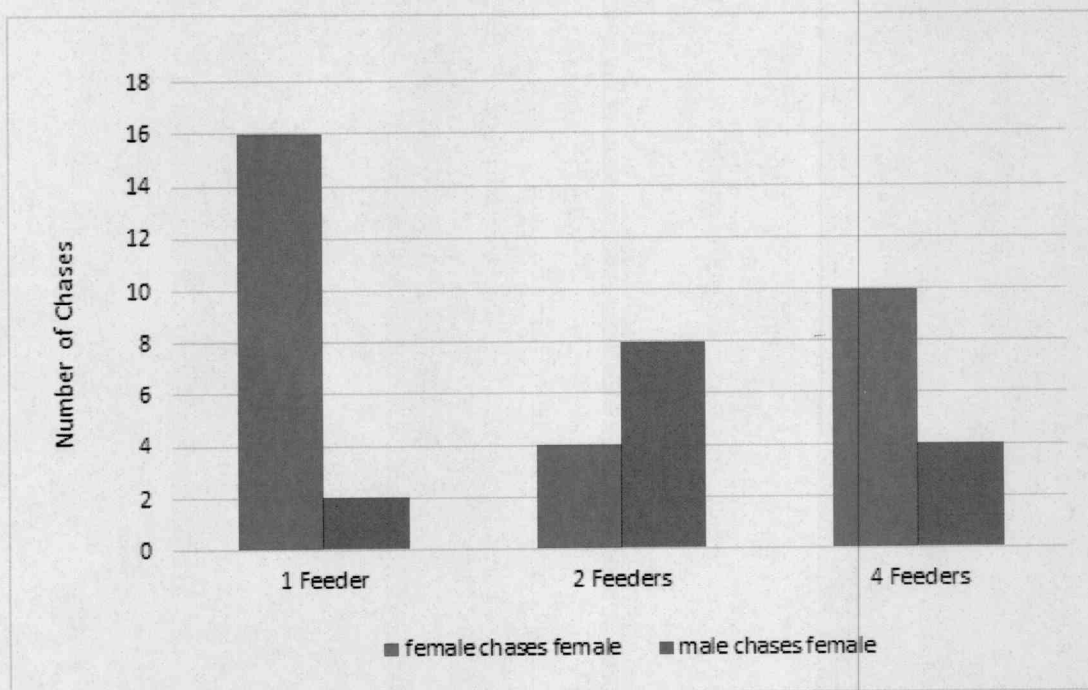


Figure 6: Number of female-female and male-female chases observed, categorized by the type of feeding site.

Discussion:

When analyzing the visitation rates among the different feeder sites for both males and females, we determined that males showed a clear preference toward the sites with more feeders. This may be because males that are able to hold richer territories are more desirable for potential female mates (Biswas et al. 2014). The preference among females was less clear, although there was some evidence that the females preferred the 4-feeder sites over the other two types. This again may be due to mating preference (Biswas et al. 2014). A clearer relationship from these data may be seen with a larger sample size.

From our results, we determined that the sex of the bird chasing and the sex of the bird being chased was more significant in combination with the number of feeders per site. On its own, the number of feeders that are present did not have an affect on the overall chasing behavior of hummingbirds. One possible explanation is that males and females have different territorial behavior depending on resource availability; analyzing male and female behavior together would be insignificant. This is further supported by the significance we found within the female-female chases. Male-female chases were insignificant, not necessarily due to data, but rather to a low sample size, as we can see trends in the male-female data. Further rationale for greater observation of female-female chases is since males are more territorial, females are left to compete for mates that have already established a territorial range. This is exhibited through a greater frequency of chasing behavior among females.

We also recorded several instances of courting in our observations. Males perform a specific courtship behavior in the presence of females, which involves a u-shaped flight pattern.

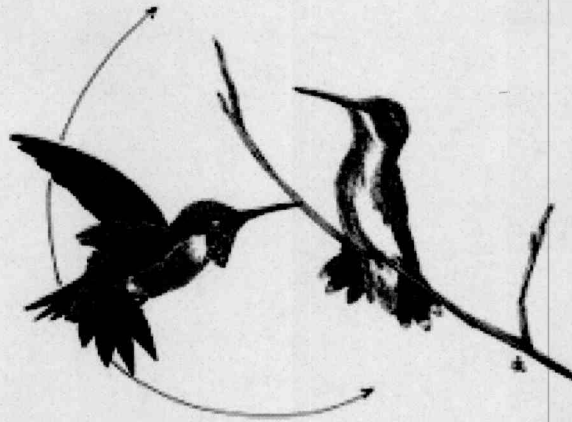


Figure 7: *Ruby-throated Hummingbird courtship flight pattern (Zickefoose, 2013)*

We observed one instance of courtship at the single feeder sites and four instances of courtship at the four-feeder sites. This could be explained by the higher resource availability at the four-feeder sites, although we would need more data points before defining a definite relationship. However, females are more likely to mate with males with greater resource holdings, so more courtship at these sites is expected.

The significantly greater number of female hummingbirds present and performing chasing behavior in the study may be related to the hummingbird mating system and migration pattern. Ruby-throated hummingbirds are a sexually dimorphic species and perform polygynous mating behavior (Wolf 1969). Concurrently there are more females than males in a population as the males tend to be more promiscuous during the short mating season. The mating system of hummingbirds would explain why there would be a greater number of female hummingbirds sighted during the study. In addition, our study began at the tail end of the hummingbird migration. Among the species of hummingbirds that migrate north for summer, female hummingbirds will occasionally hold on to a territory based on an abundance of food (Wolf 1969). Hummingbirds tend to gather at one point in relatively small territories, where the natural

food sources on which the birds typically feed are locally abundant but scattered into clumps. This creates intense intraspecific competition within territories over resources (Wolf 1969). Nevertheless, as there is an abundance of food in the area that can be defended, it is only advantageous to defend a territory over a short period of time (Wolf 1969). As the hummingbirds continue their migration through northern Michigan, there is turnover in territories and the number of undefended areas decreases. Intruding individuals are typically chased away and not allowed to feed freely at defended resources; female hummingbirds are pressured to either defend a territory or to leave the region completely and search elsewhere for a more plentiful source of food (Wolf 1969). Furthermore, female territoriality is frequently reported near nesting sites (Wolf 1969). While there is no significant data on the extent of nesting territories or their spatial relationships to dispersion patterns of the available food supply, female hummingbirds are known to build their nests approximately 2 m off the ground (Wolf 1969).

Human error likely had the biggest impact on skewed results. There were several instances of chasing where the observers were unable to identify the sex of the bird. These would have been valuable data points if the birds were able to be identified. For future studies, it would be beneficial to have more observers placed at each site. A video camera recording the observation periods would also help to reduce error as the sex of the birds could be verified after the observation period. Another potential source of error came from the difference in hummingbird feeders. While we made sure that each feeder was the same color, the feeders varied in shape, size, and material. Some feeders were glass and some were plastic. In addition, the translucent red plastic that was used to cover some feeders could have caused an aversion as the texture was different than that of the uncovered feeders. In the future, ensuring that all

feeders are identical would eliminate this error. Weather was another variable that could have affected the frequency of hummingbird visitation and chasing behavior. There was noticeably less activity on windy and rainy days than on calm and clear days. While one cannot change weather conditions, choosing only to observe on clear, calm days would create a more consistent data set.

There are many adjustments that could be made to enhance the results of this study. Most importantly, an increase in the number of observation periods would increase sample size and decrease error. Since the observation days were spread out over several weeks, the time of the bird migration and abundance of hummingbirds could have impacted hummingbird behavior. If possible, observations every day rather than twice a week would provide more consistent data during the migration as significant changes in behavior would be noticed. Likewise, it would be beneficial to encompass the entire migration period in the study and to run the study over a longer period of time. Hummingbird densities change throughout the migration period, and we would expect territorial behavior to be less in low densities than in high densities due to an increase in intraspecific interference competition. A greater difference in feeder abundance could provide more significant results in territory preference. Using sites with one feeder and five feeders would provide a more concrete differentiation between low and high richness. Additionally, changing the locations of the feeding sites relative to each other could also be beneficial to the results. The feeders were located 50 m apart from each other around the perimeter of the field. This distance was relatively short between feeding stations, so the hummingbirds sometimes flew directly from one feeder to another. However, we analyzed our results as if each feeding site was isolated. Placing the feeding sites further apart from each other

would have decreased the interactions between sites and could have given us a more realistic picture of the interactions at each individual feeding site. Changing the location of feeders would also be beneficial for increasing visitation rates. One previous study placed the feeders along the shore of Douglas Lake at UMBS and experienced much higher rates of visitation (Adams et al. 2014; Biswas et al. 2014). Although we initially changed the location to the field to avoid wind interference, there was a significant amount of wind experienced along the edges of the field as well.

In addition, it would have been helpful to identify individual birds based on a marking and tracking mechanism. We were unable to determine if the high rates of visitation on some days were due to high numbers of birds or one bird guarding the feeders. In future studies, marking the birds would allow the researchers to account for guarding behaviors (another measure of territorial behavior) and allow for an estimate of the population size. If we were able to determine the population size, we could better explain the comparably low rates of male visitation and the extremely low male-male chasing behavior.

Lastly, it would be interesting to look at hummingbird behavior through an evolutionary viewpoint to determine if the individuals who perform more territorial behavior in the higher richness sites have greater fitness. To look at fitness, we would determine the nests of the higher richness individuals in comparison to the lower richness individuals. The number of eggs produced, the number of viable hatchlings, and the number of those hatchlings that survive to adulthood could be recorded and analyzed. A higher number of successful offspring indicates higher fitness of the parents, which may suggest directional selection towards a more territorial species.

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