

# Learning and Spatial Memory in Ruby-Throated Hummingbirds (*Archilochus colubris*)

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University of Michigan Biological Station

EEB 381, General Ecology

June 15th, 2017

Prof. Joel Heinen

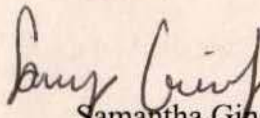
## Abstract

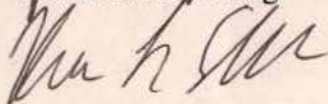
Hummingbirds have the highest mass specific metabolism of any known vertebrate. These small birds are also known to fly extraordinary distances during migration. As a result of these pressures, hummingbirds require an incredible amount of energy. It is therefore imperative that hummingbirds quickly learn and remember the locations of high energy food sources. The purpose of this study was to observe the learning period and spatial memory exhibited by Ruby-throated Hummingbirds (*Archilochus colubris*). An additional objective was to identify and understand the cues used by the birds to find the energetically rewarding feeders. It was predicted that hummingbirds would primarily use spatial memory to find high-energy food sources. The results suggest Ruby-throated Hummingbirds have a learning period of about one hour and that they may use multiple senses to efficiently find food sources.

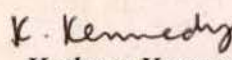
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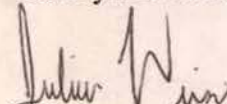
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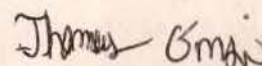
Signed,

  
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## Introduction

Hummingbirds require sugars in floral nectar to fuel their energy-intensive lifestyles (Montgomerie, 1984). The resting metabolic rate of hummingbirds is significantly higher than the expected value for non-passerine birds (Krüger et al., 1982). This high metabolic rate puts tremendous pressure on hummingbirds to seek energy-rich sources of food and requires hummingbirds to learn to feed quickly and efficiently (Diamond et al., 1986).

The Ruby-throated Hummingbird (*Archilochus colubris*) is the only species of hummingbird in eastern North America. In addition to being a sexually dimorphic species, identifiable by the bright red throat of the male birds, the Ruby-throated Hummingbird is the only known species of hummingbird to cross a large geographic barrier, the Gulf of Mexico, in one flight (Németh & Moore, 2012). This journey puts a high energetic demand on the birds' small bodies. When the hummingbirds arrive to their summer destinations, there is a premium on feeding, and it is crucial that they quickly identify a high-energy food source (Courter et al., 2013).

In the wild, hummingbirds must process many informational cues including the color, shape, and height of flowers in order to effectively find energy sources (Miliar, 1985). Hummingbirds have been shown to utilize spatial associations and landmarks to ensure that they are visiting energetically rewarding feeding sources (Brown & Gass, 1993). For example, in a laboratory study of spatial memory of Rufous Hummingbirds (*Selasphorus rufus*), six male birds initially showed no feeding preference amongst four visually identical feeders, but later showed a feeding preference for the one feeder with the highest caloric reward (Hurly, 1996).



Episodic learning may also be a crucial tool for survival and has been studied in hummingbirds. In one study of Green-backed Firecrown Hummingbirds (*Sephanoides sephanioides*), the results showed that the birds were able to adjust feeding behaviors to optimize caloric intake based on past experiences with nectar quality, nectar renewal rate, and location (González-Gómez et al., 2011).

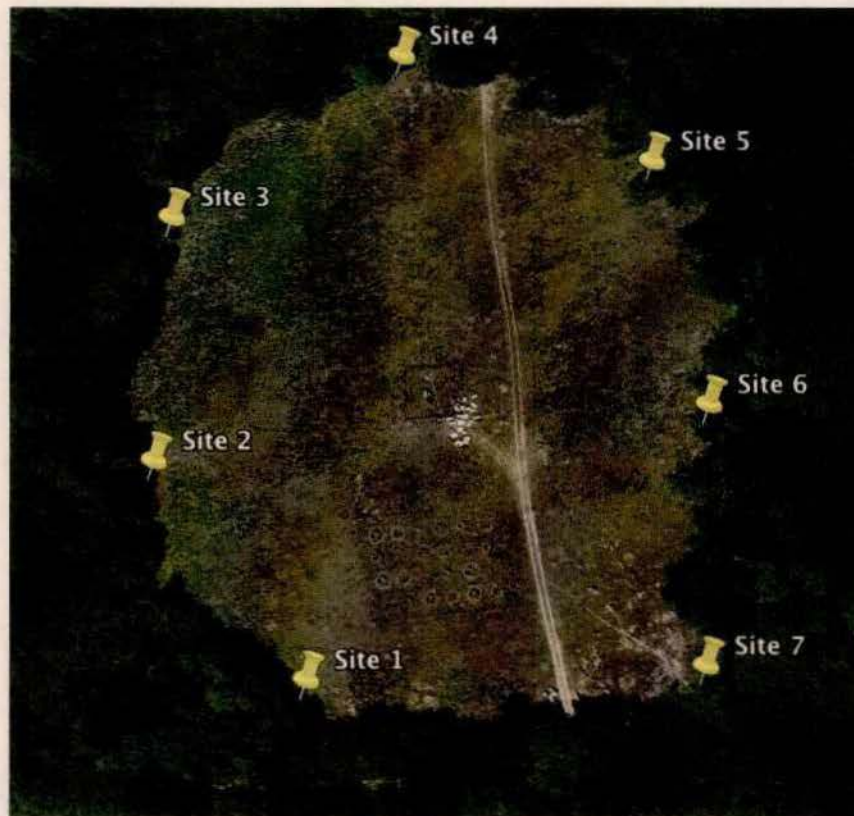
The purpose of this study was to observe the learning period and spatial memory in Ruby-throated Hummingbirds (*Archilochus colubris*). The birds were given time to learn the respective positions of a feeder with a sucrose solution and a feeder with water. It was then hypothesized that upon switching the position of these feeders, there would be a higher frequency of initial contacts at the previous location of the sucrose feeder than at the previous location of the water feeder. It was also expected that there would be a decrease in the frequency of contacts over time at the feeder that had contained water. Additionally, it was hypothesized that after learning the new respective positions of the sucrose solution feeder and the water feeder and replacing both feeders with water (to eliminate possible sensory cues), there would be a greater frequency of initial hummingbird contacts at the previous location of the sucrose solution compared to the previous location of the water, demonstrating spatial memory.

## **Materials and Methods**

In order to examine the hummingbirds' learning patterns while feeding, seven experimental sites, with two feeders per site, were placed in the UVB field at the University of Michigan Biological Station, located in Pellston, Michigan (Figure 1; Heinen & Vande Kopple, 2003). The UVB field is an open circular field surrounded by a mix of coniferous and deciduous forest. The sites were placed along the edges of the forest surrounding the UVB field, as open



woodlands are the preferred feeding grounds for Ruby-throated Hummingbirds (Pettingill, 1974).



**Figure 1.** The UVB Field at the University of Michigan Biological station and the location of the seven experimental sites used for the study (indicated with yellow pins).

The sites were placed 60 m apart with 10 m between the feeders at each site. This 60 m distance was a precaution taken in order to reduce the possible confounding variable of territorial disputes over the food source (Marquez-Luna et al., 2015). The individual feeders at the sites were placed 10 m apart from one another in order to ensure the hummingbirds' decision to feed at one feeder over the other was deliberate.

The feeders selected for the study were identical and specific to hummingbirds. That is, the feeders did not have perches so that only hummingbirds, which hover when feeding, would be able to feed on the sucrose solution. Feeders were hung primarily from white and red pine



branches 1.5 m off the ground in order to ensure uniformity. Some feeders were also hung from beech trees in order to maintain proper spacing of the feeders and sites.

For the first experimental setup, at each of the seven sites, one hummingbird feeder was filled with tap water and the other feeder was filled with a 20% sucrose solution by mass (Figure 2; Montgomerie, 1984). The sucrose and water feeders were placed randomly on each side (left or right) at each of the seven sites. For four consecutive days (May 30, 2017 - June 2, 2017), pairs of students observed one site for a period of 20 minutes total at 06:30 and for an additional 20 minute period at 19:00 EDT. Each group first observed the feeder containing the sucrose solution for 10 minutes and recorded the number of contacts (determined by the number of times a bird's beak went into the feeder). The observers then repeated the same protocol for the water feeder. The observers also recorded crossover from water to sucrose and vice versa. During this experimental setup, the only contacts that were observed were at the sucrose solution. This means that the learning period for the hummingbirds occurred between the first observation, in which no birds were observed, and the second observation, in which a 100% preference for sucrose was observed. Because the learning period was missed, these data were not analyzed.

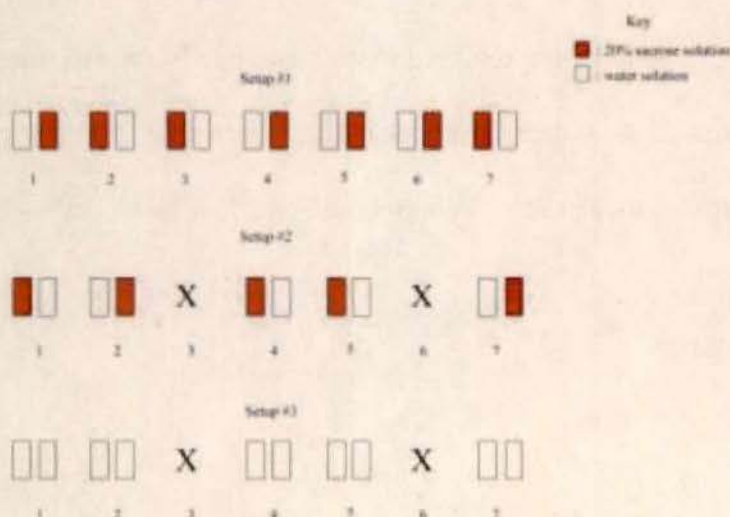
For the second experimental setup (Figure 2), all of the feeders were taken down at sundown on June 2nd after the hummingbirds had stopped feeding for the day, as a result of their torpor state (Hiebert, 1993). On the morning of June 3rd, all feeders were refilled with solutions made the previous night. At sunrise, the feeders were returned to the same tree limbs that they were taken from; however, the locations of the sucrose and water solutions were switched at each site. The activity of the hummingbirds was then observed continuously for four hours. Every



contact at each feeder was recorded, as well as the sex of the hummingbirds, the time of contact, and each time a bird crossed over from one feeder to the other at one site (a cross-over event).

In this variation of the experiment, site 3 and site 6 were removed from the experimental setup, as they had the smallest number of hummingbird contacts in the first five days of data collection. The removal of these sites allowed for more observers to watch the remaining feeders simultaneously (one observer watching each feeder), so that no hummingbird activity was missed. The feeders were left up for three days between experimental setups 2 and 3 so that the hummingbirds integrated the new feeder positions into their regular feeding patterns.

For the third experimental setup (Figure 2), the 10 feeders were taken down after sunset, washed, refilled with tap water, and replaced in the field the next morning at 06:00. Each team watched two feeders simultaneously for 2 hours, beginning the observation time at 06:00 on June 7, 2017. The objective of the third experimental setup was to test whether the Ruby-throated Hummingbird uses landmarks to memorize the location of rewarding food sources in the absence of potential olfactory stimuli. In addition to the feeder first visited, observers recorded the sex of the hummingbird, the number of contacts it made at each feeder at each site, and crossover between feeders at the same site. After recording data for two consecutive hours, the feeders were taken down from each site.



**Figure 2.** The setup of the seven experimental sites for each of the three experimental setups. The red boxes represent the feeders with the 20% sucrose solution and the white boxes represent the water feeders. The "X" marks indicate where sites were removed from the experimental setup.



A spectrophotometric test was run on both the sucrose solution and water solution to determine whether or not the solutions appeared visually different from one another. A Purge and Trap volatility test was also performed on the sucrose solution and a columbine flower (*Aquilegia*) to determine whether there is a common olfactory cue emitted by the two energy sources.

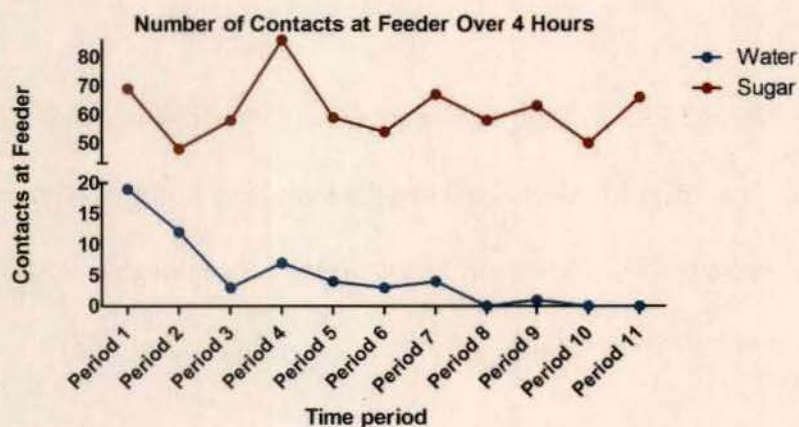
Data were analyzed using SPSS statistical software to perform Chi-square goodness of fit tests. The Chi-square tests examined differences between the frequency of initial contacts between the two feeders at one site. The Chi-square test was also used to examine differences in the frequency of contacts over time for a specific feeder.

## Results

In experimental setup 2, the hummingbirds initially visited the feeders that had contained water significantly more often than the feeders that had contained sucrose ( $X^2=89.221$ ,  $p<0.01$ ). This seems to indicate that spatial memory was not their only learning cue employed when feeding. If spatial memory had been the only learning cue, then the birds would have initially visited the feeder that had contained sucrose more frequently.

There was a significant decrease in the frequency of hummingbird contacts at the water feeder on Saturday from the first 20 minute period to the third 20 minute period, indicating a period of learning that took place in the first 60 minutes ( $X^2=11.636$ ,  $p<0.01$ ). Tests run comparing subsequent 20 minute intervals did not show a significant difference (third period vs. ninth period,  $X^2=1.00$ ,  $p=0.317$ ; third vs. fourth period,  $X^2=1.600$ ,  $p=0.206$ ). This suggests there were no other periods of learning other than the initial three 20-minute periods (Figure 3). Additionally, when both feeders contained water (setup 3), the hummingbirds initially visited the

feeders that had contained sucrose significantly more than the feeders that had contained water ( $X^2=30.421$ ,  $p<0.01$ ). This indicates that they were using spatial cues to remember the position of the energy-rich feeder.



**Figure 3.** The number of hummingbird contacts at the sucrose and water feeders over a span of four hours, in twenty-minute intervals. The blue line shows the downward trend of the number of contacts at the water feeder. The red line shows the relatively stable trend of the number of contacts at the sucrose feeder.

While it is apparent that spatial cues were used, other factors may have influenced hummingbird behavior. A spectrophotometric test was run and it was determined that there was no difference in the solutions that could be detected with the light frequencies seen by hummingbirds in nature. Although hummingbirds have the capability to see near ultraviolet light, the only rays emitted from the sucrose solution were high energy radiation (Goldsmith, 1980). A Purge and Trap test was also run to determine if olfactory senses could be used to detect the sucrose solution. It was determined that the sucrose solution fermented within 2 hours of being made and that volatile ethanol compounds were found in the solution.



## Discussion and Conclusions

The data from the first experimental setup shows the ability of the hummingbirds to learn the location of sucrose feeders. The hummingbirds displayed 100% accuracy in feeding at the sucrose feeders, but the learning period was not observed. The significance of these data is that Ruby-throated Hummingbirds show a highly accurate memory regarding the location of high-energy food sources and that they will continue to seek out this food source in the future.

The second experimental setup findings suggest that hummingbirds learn within a period of one hour or less. The short time to find rewarding food sources is likely an evolutionary adaptation to help Ruby-throated Hummingbirds after their long migration periods. On these journeys hummingbirds reach areas where temperatures are near freezing and therefore must incur the high cost of thermoregulation (Marsh & Dawson, 1989). This forces hummingbirds to find reliable, high-energy food sources in short time periods to maximize their net energy useage.

The data collected from setup 2, when the sucrose and water feeders were switched, showed that the hummingbirds did not initially visit the site of the solution that was previously sucrose. This finding suggests that the hummingbirds were able to use a different form of sensory perception in place of spatial memory in order to feed. The birds made significantly more initial contacts with the sucrose feeder, even though it was in the location of the feeder that had contained water. Visiting the sucrose feeder first decreased the travel time between the feeders, therefore saving the hummingbirds energy and reducing the period of time that they are exposed to predation (González-Gómez et al., 2011).

The findings from setup 3 indicate that Ruby-throated Hummingbirds may have a hierarchy of learning techniques which are used to locate energy sources. Integrating sensory



perception with spatial memory may allow the hummingbirds to find resources quickly even in the absence of one type of cue. Birds that can use many cues to find energy sources would have a higher fitness compared to birds that cannot. In a recent study on episodic memory, it was shown that cognitive performance varied among individuals, implying up to 6.3-fold differences in energy gain (González-Gómez et al., 2011).

Although it was determined that the hummingbirds are not able to see a difference in color between the sucrose solution and water solution using a spectrophotometric test, the ability of hummingbirds to use other senses to discern a difference between the two solutions is still unclear. The volatility of the sucrose solution indicates that hummingbirds may be able to use olfaction to detect an energy source emitting ethanol compounds. A sample of a columbine flower (*Aquilegia*), which is a preferred nectar source for Ruby-throated Hummingbirds, also emitted ethanol compounds in the Purge and Trap volatility test. It is possible that they learned to smell the difference between the solutions (Strong, 1960). In a study, Black-chinned Hummingbirds (*Archilochus alexandri*) learned to associate the odor of ethyl butyrate with a sucrose solution, even though they were able to learn a color association to the sucrose in a third of the time (Goldsmith & Goldsmith, 1982). Hummingbirds have a sense of smell but rarely use it in nature because they typically use visual cues to find food sources (Brown & Gass, 1993). They are capable of using their sense of smell, but it is unclear how much of a factor this plays in learned behavior.

Multiple confounding variables may have limited the accuracy of each experimental setup. Not being able to tag the birds and subsequently keep track of them prevented observers from distinguishing between individual birds that made contacts at each of the feeders. It is



therefore difficult to definitively conclude that the birds took an hour to memorize the location of the rewarding feeders. The observed learning period may have been inflated due to the fact that individual birds feed at different times during the day.

At the end of the first experimental period, it was observed that ants were on both the outside and the inside of all the sucrose feeders. The presence of ants on the sucrose feeders could have influenced hummingbird behavior in two main ways; the ants could have provided a visual signal that their presence was a product of attraction to the sucrose, or they may have enticed the hummingbirds to come to those feeders to gain an additional meal while feeding on the sucrose. While hummingbirds depend on nectar to survive, a critical part of their diet is the consumption of insects. Ornithologists estimate that up to 80% of a hummingbird's diet consists of spiders, flying ants, and other insects (Everett, 2011). The ants present in the sucrose feeders would not have influenced the rate of learning in the hummingbirds because they were not there until hours after the feeders were placed. However, they may have provided an additional marking to reinforce memory of the location of the sucrose feeders.

Minor confounding variables were also encountered. While observing the hummingbirds, observers sat at a distance of about 30 m from the feeders, which made it difficult to see the backsides of the feeders. If the hummingbirds visited a well that faced away from the observer's position in the field, the contact at the feeder could have been missed. If this experiment were to be performed in the future, a pair of observers at one site should sit at least 10 m apart so that they are at an angle which allows them to collectively see all four wells on the feeder.

There are several possibilities for future experimentation that would further explore learning patterns in Ruby-throated Hummingbirds. One possibility is to test the ability of the



hummingbirds to smell ethanol compounds, to determine whether olfaction could be a factor in their learning process. Additionally, an experiment testing whether the presence of insects is an indicator of high-energy nectar to hummingbirds could provide clarity on whether hummingbirds can learn to associate the presence of insects with their food source. Our study demonstrates learning in Ruby-throated Hummingbirds and explores the possibility that hummingbirds take advantage of multiple sensory cues, especially sight and sense of smell, to aid in efficient feeding.

### **Acknowledgements**

We would like to thank Professor Joel Heinen, Kathryn Braddock and Alejandro Garcia for their outstanding support and guidance throughout this study. We would also like to thank Professor Dave Ewert, Doctor Ben Jellen, Tim Veverica, Nick Gabry, Zoe Goodrow, Allison Hellman, Kyra Jamison, and Caleb Kaczmarek for their assistance in the data collection process. Finally, we give our thanks to the University of Michigan Biological Station for their support, for funding our materials, and for allowing us to use their land for the project.



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