Wilson Bull., 92(1), 1980, pp. 53–62

EXPERIMENTS IN FEEDING BEHAVIOR OF THE ANNA HUMMINGBIRD

THOMAS G. WHEELER

The reports on hummingbird color preference range from red dominance to blue dominance (Clark 1902; Pickens 1930, 1941; Bene 1941, 1946; Sherman 1913; Poley 1968; Stiles 1976). Such differences in preference may be due to the particular species studied, differing experimental conditions or the bird's ability to learn the most rewarding color (Bene 1941, 1945; Collias and Collias 1968). These reports do have one strong feature in common: each assumes, suggests, or attempts to demonstrate the significance of color preference in the bird's ability to survive. The studies reported herein attempt to answer some basic questions, as well as to elucidate when the bird normally feeds, its ability to learn and its color preference. Unlike most previous studies, my investigation was done on a large population of Anna Hummingbirds (*Calyptie anna*) in the wild. Four separate studies of Anna Hummingbird feeding behavior have been performed: (1) to determine temporal patterns of feeding; (2) to determine if the color or location of a food supply was the controlling factor in attracting the animals to feed; (3) to determine how rapidly the animal could learn the location of a new food supply (or an adversive substance); and (4) to determine if the birds were differentially attracted to various colors.

METHODS

All studies reported here were done at Camp Nelson, California, the High Sierras (elevation 1500 m) during mid-July 1976. The days were warm (23–27°C) with clear skies, unless otherwise noted. The study site was in front of an old cabin where for years hummingbird feeders had been placed and serviced with red colored sugar water. Several species frequented this site.

Temporal feeding schedule.—The feeder used in this experiment, a hanging gravity feed device, with small (1.5 mm) holes in the gray metal base, had been in use for 5 years in the same location. The fluid container (250 ml capacity) was made of clear glass and was filled an average of 3 times per day with a solution of saturated sugar water, using commercial pure cane sugar. All drinks taken by all feeding birds were recorded on a counter, that was read every 15 min throughout the day. Counts taken between 08:00 and 11:00 may be somewhat low; some counts may have been missed due to the high concentration of birds.

Attraction to color or location.—The above experimental setup was varied only by changing the color of the saturated sugar solution in the feeder every 15 min. Sixteen independent test sequences were done and in each sequence 5 colors (red, yellow, green, blue, clear) were presented in random order. Therefore, the color of the solution was changed a total of 80 times providing 16 exposures for each color. Each colored solution contained 15 drops of food color (McCormick brand) per pint of water. For the purpose of experimental repeatability the transmission spectrum was determined for each of the solutions (Fig. 1) with a Cary dual

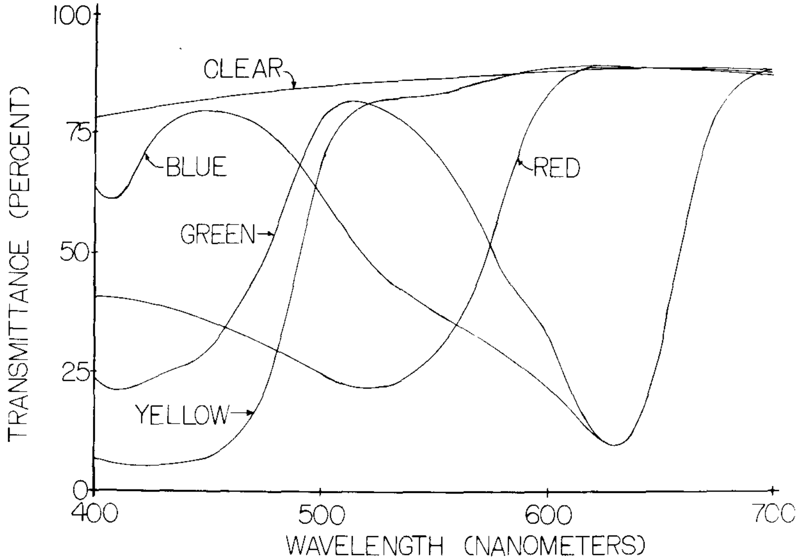

FIG. 1. Spectral transmission curves obtained from samples of the 5 colored sugar solutions used. The sample path length was 1 cm; a proper labeling should therefore be "percent transmittance per linear centimeter" since light scattering was not taken into account.

beam spectrophotometer. The experiment took approximately 26 h and was done between 08:00 and 17:00 on 3 consecutive clear days.

Learning location of a food supply (or adversive substance).— For this experiment the birds were given a choice between 2 identical containers (open-top pint-sized canning jars made of clear glass). One container was filled with water and the other with a saturated sugar solution (both clear). The containers were placed in a location not previously used. Counts were made on birds that approached the container from a distance of at least 1.5 m, and the container from which the bird drank first was recorded. Birds often went from the initial container to the second container (by choice or forced by aggressive birds). Only the bird's first choice was counted.

The experiments designed to determine the bird's response to an unpleasant/adversive substance was done using only a single container at the same location as the previous study. Feeding was permitted to continue until the number of drinks per 5 min period reached steady state. The sugar solution was then replaced with a saturated solution of sodium chloride. The time of replacement was designated time zero (t = 0) and counts were taken of the number of drinks from the container during each 5 min interval thereafter. All counts were taken between 08:00 and 22:30 on 2 consecutive sunny days.

Color preference.—In this study, the same concentrations of sugar and food coloring were used as those described in the experiment on attraction to color or location. All colors were presented simultaneously. Five identical containers were placed side by side in a straight line in a previously unused location to obviate location recall. The color sequence was changed every 15 min. Fifteen sequential arrangements were used, and efforts were made to ensure that each container received equal exposure at the end positions (see Results) and

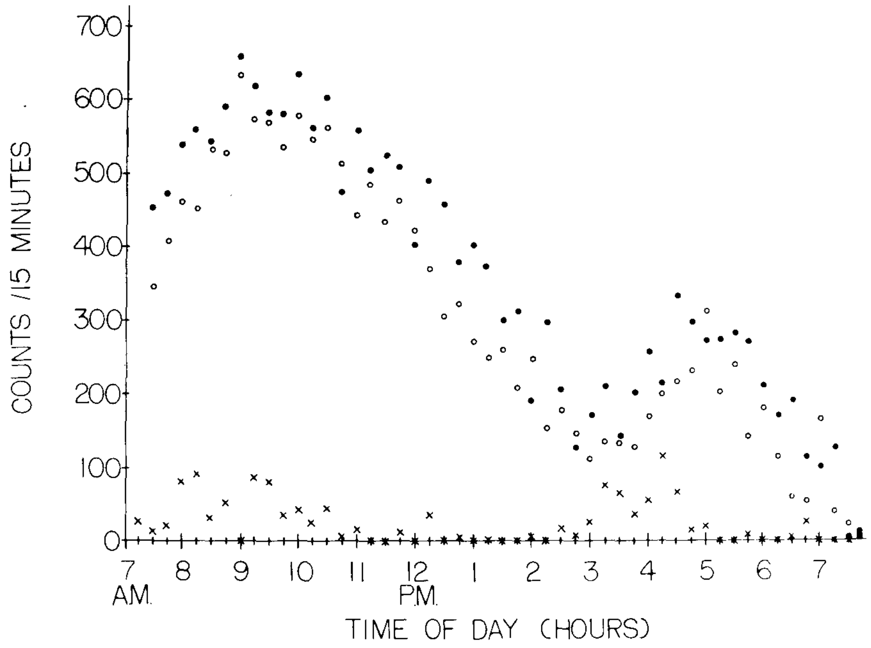

FIG. 2. Concentration of Anna Hummingbirds' feeding on a nectar substitute as a function of time of day. Each data point represents the total number of drinks taken during the preceding 15 min intervals. Data were collected on 3 consecutive days. Day 1 (●) was sunny and warm, the mean number of counts (over the entire day) was 354 ± 179. Day 2 (○) was partly cloudy and had a mean of 301 ± 177. Day 3 (×) was overcast and rainy and displayed a drastic reduction in the total and mean (24 ± 30) number of counts.

that no 2 colors were sequentially adjacent. Counts were made on birds which approached the containers from a distance of at least 1.5 m and scores were kept with respect to the container each bird sampled first. The experiment was conducted between 08:30 and 10:30 on 2 consecutive clear days.

RESULTS

Temporal feeding schedule.—Fig. 2 shows the results obtained from 07:15–20:00 on 3 consecutive days. The day-to-day differences observed in temporal feeding habits were related to the weather conditions. Day 1 was sunny, clear and warm (high 28°C), whereas day 2 was partly cloudy, breezy with a high temperature of 23°C. This difference in weather conditions appears to be reflected in the birds' feeding behavior in that almost every count taken on day 2 was lower than that obtained on day 1. The general shape of the curves for days 1 and 2 were the same. The data taken on day 3, however, were quite different. Day 3 was overcast, light

TABLE 1
NUMBER OF DRINKS PER 15 MIN FROM A SINGLE CONTAINER OF COLORED SOLUTION[a]

Color	Mean counts	SD
Red	292	±138
Yellow	293	±121
Green	296	±117
Blue	293	±141
Clear	275	±142

[a] Color of solution was randomly changed. The mean and SD are presented for 16 presentations of each color. A *t*-test performed on these data produced no significant difference in the birds' feeding behavior for the different colors presented.

to moderate rain fell throughout the day and the high temperature was 17°C. The distinguishing feature of day 3 was the low total count and the different distribution of counts. The increase in counts between 15:00 and 17:00 coincided with a decrease in cloud cover and rainfall. At approximately 17:00 the sky became completely overcast, and the rain increased in intensity. The total number of birds observed in the vicinity was lower on day 3 than on the previous days. However, it was noted that the majority of birds observed on day 3 spent their time around green plants, rather than the feeders, and appeared to be investigating and pecking the underside of the leaves. Sometimes birds would leave the greenery in pursuit of insects. These observations strongly suggest that the Anna Hummingbirds were feeding primarily on insects during this period.

Attraction to color or location.—The second experiment was conducted to determine if color or location of the food supply was the dominant factor in feeding behavior. Eighty independent test intervals are included in these results (Table I). The only solution which appears to have received somewhat less attention than the others was the clear solution. This reduced use may have been due to resemblance of this latter container to an empty container.

The large standard deviation for each color (Table I) reflects the different concentrations of birds feeding at different times of the day. For example, the data collected between 08:00 and 10:00 produced the following results: R = 660, Y = 633, G = 577, B = 618 and C = 567; whereas a color sequence done between 14:30 and 17:00 yielded much lower counts (R = 126, Y = 130, G = 136, B = 113 and C = 136). The difference in counts between the 5 colors in any one test sequence was very small, but the difference in counts for a given color across test sequences was large, reflecting differences in time of day (Fig. 2). In fact, the standard deviations reported in Table I are similar to those reported for the average counts per 15 min in the temporal study.

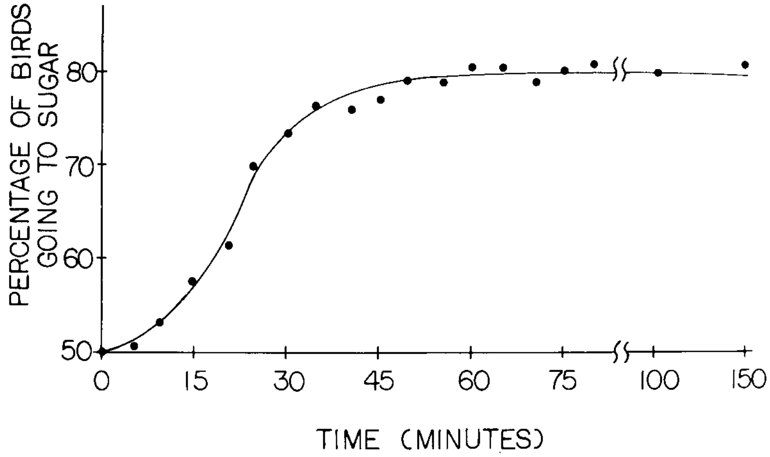

FIG. 3. Learning behavior of birds when given a choice between 2 feeding containers placed side-by-side; one with sugar water and the other with just water. Each data point was computed using the count of birds feeding from the sugar container divided by the total number of birds feeding from both containers during the preceding 5 min intervals.

It is clear that once the animals have located a food supply, its location, not color, was the controlling variable. In fact, one could remove the food supply entirely, including the container, and the birds would continue to come to the location for hours. As the birds discovered that the food supply was no longer at that location, the frequency of investigation decreased. Invariably, however, some dominant males, seemingly protecting their "food supplies," would continue to drive off other birds that came into the vicinity. This was observed to continue for 3 days in 1 case.

Learning location of a food supply (or adversive substance).—In these experiments 2 identical containers were used: 1 contained clear water, and the other clear sugar water. Once the first bird had discovered the location, it was only seconds before large numbers of hummingbirds began approaching the containers. The initial counts I made were evenly distributed between the water and sugar containers. The plot in Fig. 3 reflects how rapidly the investigation period of the birds was replaced with feeding as the birds learned which container was filled with the sugar water. Again, once the birds had discovered a food supply, they patronized the area long after the supply had been removed. After the sugar supply was replaced with water, the ratio of birds which flew to the container which previously contained sugar water remained constant. Even some 6 h later, 80% of the birds that came to feed tested the previous sugar container first.

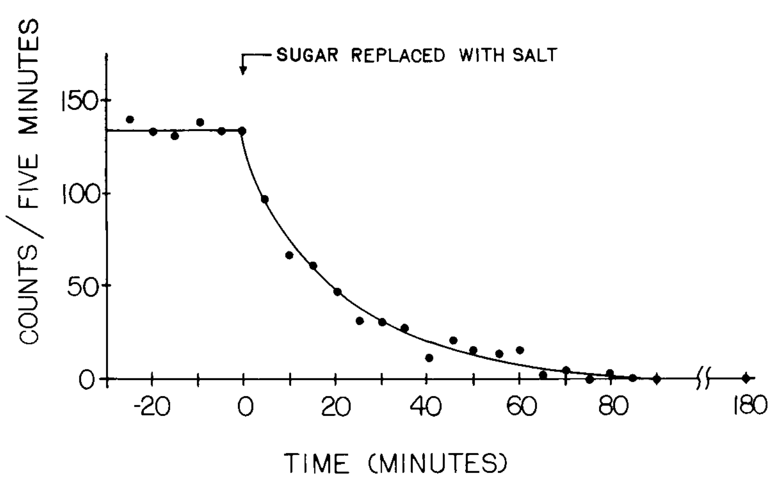

FIG. 4. Response of birds when a food supply was replaced by an adversive substance. Each data point represents the total number of drinks taken during the preceding 5 min intervals.

When the sugar solution was replaced with an adversive solution of salt, the birds quickly began to avoid the area (Fig. 4). Some individually identifiable birds learned to avoid the salt solution after a single trial. Once the bird had tested the salt it would fly away, chirping loudly and shaking its entire body and, on occasion, would even momentarily lose flight control. Some birds returned once or twice to this salt container, investigated it from top to bottom for some time, and then departed without testing the salt solution. After 3 h (t = 180), no birds were observed anywhere in the vicinity. At this time the salt solution was replaced with a clear sugar solution; it was 2 days before the birds began to return and feed from the container.

Color preference.—A distinction must be made between the bird's ability to recall the location of the food supply and the attractiveness of a particular color during a food search (Bene 1946). The second experiment showed that once the location of a food supply had been discovered, the color of that supply was irrelevant to the feeding behavior. Therefore, this experiment was designed to determine which color the birds were most attracted to when in search of food. The birds did respond differently to color of a food source, red being the preferred color (Table 2A). The significance levels calculated for each color combination are shown in Table 2B.

TABLE 2

A AVERAGE NUMBER OF BIRDS APPROACHING AND DRINKING FROM EACH OF 5 CONTAINERS CONTAINING DIFFERENT COLORED SOLUTIONS[a]

Color	Mean counts	SD
Red	33.9	±8.7
Yellow	13.1	±5.0
Green	8.4	±2.7
Blue	4.3	±1.7
Clear	5.3	±1.6

B RESULTS OF STUDENT *t*-TEST ON ABOVE DATA

	Y	G	B	C
R	0.001	0.001	0.001	0.001
Y	—	0.015	0.001	0.01
G	—	—	0.001	0.015
B	—	—	—	0.015

P value

[a] Containers were in a straight line; order was randomly changed every 15 min.

DISCUSSION

A number of authors suggest that nectar is a primary food source for hummingbirds and that the innate attraction for these birds to particular colors is a major factor in their ability to survive. The feeding behavior of hummingbirds would appear to be much more complex when one considers the ability of the birds to rapidly learn the location of a colorless food supply and to recall the location of food for a long period as well as the striking correlation between the number of birds feeding on a nectar substitute and time of day and changes in the weather. Considering the data reported here, the factors controlling the Anna Hummingbirds' feeding on a nectar source may be placed in the following order: (1) time of day, (2) weather, (3) location and (4) color. Obviously, other factors influence feeding behavior and need to be considered as controlling factors. These might include number or type of flowering plants, quantity and quality of nectar and energy expenditure (Stiles 1976).

Given that the weather and time of day are favorable, my studies indicate that location, not color, was the most important parameter in the birds' feeding on a nectar source. Indeed, it would be most efficient in terms of energy expended if the location of food source was known and easily recalled (Stiles 1971). As shown in this series of field experiments hummingbirds are capable of rapidly locating a food source and do not readily forget that location. It was repeatedly noted that the birds in search of a food source investigated (seemingly at random) everything in sight—color, shape, size, or material makeup seemed to make little difference. Once a food supply was located, all attention was directed to it. Therefore, it appears that when a hummingbird is among familiar surroundings, memory of location undoubtedly guides it to a large degree in its feeding. From the color preference study, it is clear that Anna Hummingbird has the ability to locate a red food supply more efficiently, on the average, than green or blue supplies. However, a new food supply of clear sugar solutions placed in unfamiliar locations, was also located rapidly by the birds. As noted above, the time of day and weather appear to be the major controlling factors as to whether the bird feeds on a nectar substitute at all.

Anna Hummingbirds are known to feed on small insects during the warm part of the day and on overcast, rainy days (Gander 1927, Bene 1946). In my study, frequency of feeding from the nectar substitute decreased from 11:00 to 15:00; data obtained on an overcast, rainy day (day 3) showed a tremendous reduction in feeding on the nectar substitute and the birds appear to be in search of other food supplies during this period. This confirms previous observations. The ratio of arthropods to nectar consumed by the Anna Hummingbirds is unknown. Henderson (1927) found that the stomach contents of 111 Anna Hummingbirds comprised: Diptera, 45%; Hymenoptera, 35%; Hemiptera, 17%; spiders, 2%; fruit pulp, a trace. Clark (1902) found that 1 stomach contained 32 treehoppers, 1 spider, 1 fly and other insect parts. The proportion of liquid food in the ordinary diet of the bird cannot be determined by an examination of stomachs, but these data do indicate the bird's need for large quantities of animal protein (Lucas 1893). It has also been reported that Anna Hummingbirds often follow sapsuckers (*Sphyrapicus* sp.) from tree to tree (Woodbury 1938). The hummingbird visits each puncture that the sapsucker makes in the bark and partakes of both sap and small insects that have been attracted to it (Grinnell and Storer 1924). Indeed, attraction to a carbohydrate nectar source may also be for the purpose of feeding on small insects living in flowering plants. The observation that hummingbirds consume a large quantity of food other than nectar is consistent with the known nutritional requirements of other vertebrates. Caution must be taken if nectar is to be considered the hummingbirds' primary food source. Nectar probably serves as a water supply as well as a convenient source of carbohydrates and insect habitat. No alternate source of water has been reported.

A number of questions remain. Why are the birds away from the nectar source for such extended periods during the day? Why does weather play such an important role? Does the Anna Hummingbird frequent different flowers due to nectar quantity, quality or color, or does it do so because insects are more abundant on these plants? Experiments are in progress that may provide answers to some of these basic questions.

SUMMARY

In my studies the Anna Hummingbird fed on a nectar substitute primarily in the early morning. The quantity of nectar consumed increased steadily until 09:30 and decreased thereafter. There was also a short feeding period between 16:00 and 18:00. The quantity of nectar consumed appeared related to weather conditions. Maximum consumption was on clear days, with decreasing consumption with increasing cloud cover. During periods of rainfall, even light drizzle, many birds remained in the vicinity but apparently switched from nectar to feeding on small insects.

C. anna appears to have a keen ability to recall the location of a food source. Sugar containers placed in new locations were rapidly located by the study population. Even when identical containers were placed side-by-side, 1 with and 1 without sugar, the birds learned to distinguish between them. Once a nectar source was located, the color of the source had no effect on the number of birds approaching it, or feeding from it, as demonstrated by repeated changing of the color of the sugar solution. Irrespective of the color of the solution, including clear liquid, the same number of drinks were taken per unit time. The animals did discriminate among colors when 5 colors were presented simultaneously in 5 identical containers placed side-by-side and randomly rearranged in order to avoid location preferences. Anna Hummingbirds approached, and fed from, the red container more frequently than the yellow, green, clear and blue containers (in order of decreasing frequency).

Considering the above observations, the factors controlling the Anna Hummingbirds' feeding behavior, in order of importance, are: (1) time of day, (2) weather, (3) familiarity of the location of the source and (4) color of the source. It is not known what percentage of the bird's diet consists of nectar. Anna Hummingbirds may be attracted to nectar sources in order to feed upon insects that abide there, or, as a source of water.

ACKNOWLEDGMENTS

The constructive scientific reviews by my colleagues are gratefully appreciated. In addition, may I thank Hazel Magill and the Robb family for their gracious hospitality and the use of the mountain cabin. Miss Lillian Robinson provided not only the inspiration, but also intellectual instruction, which ultimately led to the research reported here.

LITERATURE CITED

BENE, F. 1941. Experiments on the color preferences of Black-chinned Hummingbirds. Condor 43:237–323.

———. 1945. The role of learning in the feeding behavior of Black-chinned Hummingbirds. Condor 47:3–22.

———. 1946. The feeding and related behavior of hummingbirds. Mem. Boston Soc. Nat. Hist. 9:403–478.

CHAPMAN, D. 1972. The role of fatty acids in myelin and other important brain structures.

Pp. 31–57 *in* Lipids, malnutrition and the developing brain. Associated Scientific Publishers, New York, New York.

CLARK, F. C. 1902. Food of Anna Hummingbird. Condor 5:18.

COLLIAS, N. E. AND E. C. COLLIAS. 1968. Anna's Hummingbirds trained to select different colors in feeding. Condor 70:273–275.

GANDER, F. F. 1927. The fly-catching habits of Anna Hummingbird. Condor 29:171.

GRINNELL, J. AND T. I. STORER. 1924. Animal life in the Yosemite. Univ. Calif. Press, Berkeley, California.

HENDERSON, J. 1927. The practical value of birds. MacMillan, New York, New York.

LUCAS, F. A. 1893. The food of hummingbirds. Auk 10:311.

PICKENS, A. L. 1930. Favorite colors of hummingbirds. Auk 47:346–352.

———. 1941. A red figwort as the ideal Nearctic bird-flower. Condor 43:100–102.

POLEY, VON D. 1968. Experimentelle Untersuchungen zur Nahrungssuche und Nahrungsaufnahme der Kolibris. Bonn. Zool. Beitr. 19:111.

SHERMAN, A. R. 1913. Experimenting in feeding hummingbirds during seven summers. Wilson Bull. 25:153.

STILES, F. G. 1971. Time, energy and territoriality of the Anna Hummingbird (*Calypte anna*). Science 173:818–821.

———. 1976. Taste preferences, color preferences, and flower choice in hummingbirds. Condor 78:10–26.

WOODBURY, A. M. 1938. Red-naped Sapsucker and Rufous Hummingbird. Condor 40:125.

DEPT. OPHTHALMOLOGY, SCHOOL OF MEDICINE, UNIV. LOUISVILLE, 301 EAST WALNUT ST., LOUISVILLE, KENTUCKY 40202. ACCEPTED 2 NOV. 1978.