FEEDING ACTIVITY AND COLOR PREFERENCE OF RUBY-THROATED HUMMINGBIRDS

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Pickens (e.g., 1930, 1941, 1968) has listed native and introduced plants in the Nearctic region that are regularly visited by birds. The figwort (Scrophulariacae), mint (Labiatae), and pea (Leguminosae) families contain the greatest number of ornithophilous plants, and the predominant flower color among plants visited by birds is red. Hummingbirds are by far the most important group of flower-pollinating birds in the New World and their apparent tendency to visit red flowers has drawn particular attention. In California the only flowers which are specifically adapted to pollination by hummingbirds have flower colors of some shade of red, while non-red flowers that are also visited by hummingbirds are shared with other pollinators, usually insects (Grant 1966). These and similar observations have led to the popular belief (Bent 1940; Amadon 1966) that hummingbirds have an innate preference for red, and that this has led to natural selection for red flowers among ornithophilous plants.

After an extensive review of the literature, Grant (1966) concluded that the "experimental evidence does not support the assumption that hummingbirds prefer red to other colors." Unfortunately, most of the statements made about color preference in hummingbirds have been based on field observations where there was no opportunity to manipulate variables that might affect feeding behavior, and there have been few valid experiments designed to answer this question. The available evidence suggests that the position of a food source is more important than its color (Lyerly et al. 1950; Grant 1966; Collias and Collias 1968) and that color preference can be learned if there is a differential reward (Bene 1941; Collias and Collias 1968). Even when trained to a particular color, Anna's Hummingbirds (*Calypte anna*) frequently showed "exploratory shifts" to other colors, and Collias and Collias (1968) noted that this "increases the probability that flowers of different species will be discovered to be profitable just as soon as they begin to have a good nectar flow."

METHODS AND MATERIALS

This investigation of the feeding activity and color preference of Ruby-throated Hummingbirds (*Archilochus colubris*) was conducted at Lindner Point, Emma Lake, Saskatchewan, near the northern limit of the range of this species in Canada. Artificial feeders were first installed at this locality in 1964 and have subsequently been used each summer by female Ruby-throated Hummingbirds, which also feed on nectar from native and introduced flowers in a yard where the feeders were installed. The feeders consisted of wire loops supporting 18 $\times$ 145 mm lip vials filled with a 50 per cent sugar solution.

Two feeder arrangements were used in this study. In the first series of observations (Series A), feeders were distributed throughout the yard 110–200 cm above the ground and 2.6–12.0 m apart. In the second series of observations (Series B) a rack of five feeders 10 cm apart on a 16 $\times$ 24 inch green background was installed at the location corresponding to position no. 1 in Series A. Vegetable dyes were added to the sugar solution to obtain the colors red, green, blue, and yellow, and one feeder was left clear with sugar solution but no coloring added. The feeders were refilled as often as necessary to keep the level of the food within easy reach of the hummingbirds.

The experimental design was a latin square similar to that used by Lyerly et al. (1950), except that five colors and five positions, rather than four, were used. To give independent tests of color and position, the colors were rotated among the five positions according to the schedule shown in table 1.

Observations were made for 1-hr periods at different times of the day. Temperature, wind direction and speed, cloud cover, and the time of each visit to a feeder position were recorded. A "visit" was scored whenever a hummingbird used a feeder, regardless of whether the bird only dipped its bill once and moved on, hovered and fed repeatedly at the feeder, or perched and fed for a long time. The data are arranged according to "first visits" and "all visits." If for example, a bird entered the yard or approached the rack and fed first at position no. 1, moved to position no. 3, and returned to no. 1, its "first visit" was to no. 1 and "all visits" were scored for a total of three.

RESULTS

The results of this study are based on 5020 min of observation and 687 feedings by 2–4 females, 2 July–17 August 1968.

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TABLE 1. Experimental design, showing arrangement of five colors (Y, yellow; C, clear; R, red; G, green; and B, blue) by five feeder positions.

Color arrangement	Feeder position 1	2	3	4	5
I	Y	C	R	G	B
II	B	Y	C	R	G
III	G	B	Y	C	R
IV	R	G	B	Y	C
V	C	R	G	B	Y

TABLE 3. Color preference as shown by number of visits to feeders by Ruby-throated Hummingbirds.

Experiment	Color Y	B	G	R	C	Total	Mean
Series A (yard)							
First visit	52	26**	60	39	73**	250	50
All visits	80	46**	80	76	120**	402	80
Series B (rack)							
First visit	51	46	38	59	56	250	50
All visits	86	73	86	78	111**	434	87

** $\chi^2 = 6.64$, $df = 1$, $P < 0.01$.

FEEDING ACTIVITY

Feeding activity was distributed more or less equally throughout the day. The earliest recorded visit was 04:30 (sunrise, 04:00) and the latest was 21:40 (sunset, 20:20). Feeding was not inhibited by weather except during exceptionally heavy rains or windstorms.

Table 2 shows the frequency distribution of the number of feeders visited during each of 687 feedings. The usual pattern was to fly directly to a "preferred feeder" and to return repeatedly to that feeder on subsequent visits, although there was also a tendency to make "exploratory shifts" to additional feeders or to flowers in the garden after the first feeder had been visited. On most occasions, the birds were conservative in their feeding patterns and visited only one or two feeders; at other times they explored several potential or known food sources.

It was evident that these exploratory flights are an important part of the feeding behavior of hummingbirds. They frequently investigated brightly-colored objects such as book covers, food packages, and clothing and seemed to be attracted to a great variety of colors. They also investigated plants before they were in flower and sometimes before buds were evident, apparently testing for nectar. If a vial was removed from a feeder position, that position would continue to be visited regularly when a hummingbird was making its rounds of the yard. These observations tend to confirm the conclusions (Bene 1945; Collias and Collias 1968) that hummingbirds frequently explore alternate food sources, even when a known source is available, and that they learn to recognize food sources by association with color and location.

TABLE 2. Frequency distribution of number of feeders visited at each feeding by Ruby-throated Hummingbirds.

No. feeders visited	No. visits	% total visits
1	413	61.1
2	182	26.9
3	64	9.5
4	23	3.4
5	4	0.6
6	0	
7	0	
8	0	
9	1	0.0
10	0	

COLOR PREFERENCE

As the different colored feeders were rotated daily through different positions according to the schedule shown in table 1, it was necessary for a bird to follow a color from one position to the next in order to express a color preference independent of position. Table 3 shows the number of visits to the five feeders in Series A and Series B. Each series of observations is presented separately with the data arranged according to the first feeder visited (first visit) and the total of all feeders visited (all visits) each time a bird entered the yard to feed. Observations were continued until each color and feeder arrangement in table 1 had been visited 50 times, so that the total of first visits for each series was 5 × 50 (250) and the total of all feeders visited depended upon the number of additional feeders used at each feeding.

A chi-square analysis of the observed number of visits to each color (table 3) showed that, with the colors rotated through the five positions in the yard (Series A), there were significantly fewer visits to blue and significantly more visits to clear ($P < 0.05$) than would be expected by chance, whether the analysis is of first visits or of all visits. When the feeders were grouped on a rack (Series B), the tendency for blue to receive fewer visits than other colors disappeared, and a significant preference for "clear" was shown in all visits combined, but not in first visits.

There is no apparent explanation for the expressed preference for "clear" in these tests.

TABLE 4. Position preference as shown by number of visits to feeders by Ruby-throated Hummingbirds.

Experiment	Position 1	2	3	4	5	Total	Mean
Series A (yard)							
First visit	65*	33*	42	32*	78**	250	50
All visits	94	76	67	50**	105**	392	78
Series B (rack)							
First visit	53	34*	20**	38	105**	250	50
All visits	84	69	58**	87	136**	434	87

* $\chi^2 = 3.84$, $df = 1$, $P < 0.05$; ** $\chi^2 = 6.64$; $P < 0.01$.

However, in view of the ease with which hummingbirds form associations with color, taste, and food location (Bene 1941), it is quite possible that an association with a particular color might be formed before or at the start of an experiment, possibly because of the initial location of the color, and persist long enough to influence one set of results but not be sufficiently fixed to constitute a general color preference.

In order to determine whether the color selections shown in Series A and B of table 3 were similar, the paired differences were tested. The two sets of results were not similar ($P < 0.05$) and the differences could not be explained by color. We can conclude, therefore, that these hummingbirds did not show a consistently significant preference for any of these colors.

POSITION PREFERENCE

The number of visits to each feeder position, regardless of its color, is shown in table 4. A chi-square analysis of these data shows that in Series A, when the feeders were at five positions in the yard, positions no. 1 and no. 5 received significantly more first visits, and positions no. 2 and no. 4 fewer visits than would be expected if there were no position effect. In the analysis of all visits in Series A, the preference for position no. 1 and avoidance of no. 2 disappear. Positions no. 1 and no. 5 were near the edge of the yard, close to trees where the hummingbirds often perched between feedings, and were therefore the most readily accessible by the two most frequently used approach patterns. However, after a bird had paid its initial visit to one feeder, there was a tendency (table 2) to fly to other feeders in a fairly regular pattern that often included positions no. 2 and no. 3 but seldom included no. 4. This explains the change in significance of chi-square values between first visit and all visits, with position no. 5 the most frequently visited and no. 4 the most commonly excluded.

The five feeders on the rack in Series B were located at position no. 1 in Series A, so that the corresponding preference for position no. 5 in both Series A and B is fortuitous. Again, there was a significant tendency to first visit the outside position on the rack at no. 5 and to avoid the two inside positions (no. 2 and no. 3), but visits became more evenly distributed among the five positions in all visits when the birds made exploratory shifts to other feeders.

COLOR TRAINING

At the conclusion of the above experiments (Series A and B), the feeders were positioned on the rack in arrangement I (table 1) and the birds were allowed to feed without any change in the color arrangement for five days. The feeders were then emptied and refilled with sugar solution in the red feeder and unsweetened water without coloring in the others and placed in the first arrangement shown in table 5. Visits to the feeders were scored until the rack of feeders had been visited (first visit) 20 times (usually about 2 hr). The feeders were then changed to the second arrangement shown in table 5 and the

TABLE 5. Color training of Ruby-throated Hummingbirds, with sugar added to red (R+) feeder.

Color/position feeder arrangement[a] 1	2	3	4	5	No. visits/position 1	2	3	4	5	Total	% R+ choice
First visits											
C	Y	B	G	R+	3	0	1	2	14	20	70.0
R+	C	Y	B	G	14	1	0	0	5	20	70.0
B	G	R+	C	Y	1	0	18	0	1	20	90.0
All visits											
C	Y	B	G	R+	3	1	3	3	20	30	66.7
R+	C	Y	B	G	20	3	1	1	6	31	64.5
B	G	R+	C	Y	1	0	21	1	1	24	87.5

[a] Presence of sugar is indicated by +.

TABLE 6. Position training of Ruby-throated Hummingbirds, with sugar added to one (R+) of five red feeders.

Sugar/position feeder arrangements[a]					No. visits/position					Total	% R+ choice
1	2	3	4	5	1	2	3	4	5		
First visits											
R−	R−	R−	R−	R+	5	0	1	2	12	20	60.0
R+	R−	R−	R−	R−	12	1	0	1	6	20	60.0
R−	R−	R+	R−	R−	5	1	7	5	2	20	35.0
All visits											
R−	R−	R−	R−	R+	5	1	4	5	19	34	55.9
R+	R−	R−	R−	R−	20	2	4	3	7	36	55.6
R−	R−	R+	R−	R−	8	8	24	8	3	51	47.1

[a] Presence and absence of sugar is indicated by + and −, respectively.

procedure was repeated until 20 first visits had been scored at each of the three arrangements. Red was chosen for color training because it is complementary to green, the background color of the rack and of natural vegetation, and is the most conspicuous color in daylight (Pickens 1930).

The first hummingbird to visit the feeders flew first to position no. 1, moved to no. 3 then no. 4, and finally settled at no. 5 to feed. The same bird returned in 2 min and again began at no. 1, moved to no. 2 and then to the correct feeder, no. 5. It returned again in 3 min and flew directly to no. 5 and in subsequent feedings identified the correct feeder with few exploratory visits. This was the usual pattern in this experiment: the correct feeder was quickly identified and the birds almost invariably went directly to it after the first few visits, although they continued to make a few exploratory visits in search of or away from the correct feeder throughout the period of observation. In the first arrangement shown in table 5, in which the correct feeder was at the most preferred position on the rack (table 4), the correct feeder received 14 of 20 first visits for an accuracy of 70 per cent. When the feeders were changed to the second arrangement, which placed the correct feeder at the second of the preferred outside positions, the correct feeder was located in about the same amount of time and with the same accuracy. However, by the time the correct feeder reached position no. 3 in the third arrangement, red was identified as the correct feeder with 90 per cent accuracy and there were only three visits to other feeders in all visits. It is evident that the color red provided a good visual clue to accurate identification of the food source when its position was changed during the experiment.

POSITION TRAINING

In order to test the ability of the birds to identify a food source without a color clue, all five of the feeders were colored red, with sugar added to only one. Otherwise the procedure was the same as in the previous color training test. The results in table 6 show that the birds were able to identify the correct feeder by position, but with less accuracy than they achieved with a color clue. The correct feeder in the first arrangement was identified with 60 per cent accuracy in first visits and there was no significant change when the correct feeder was changed from one outside position to the other. When the correct feeder was moved to the central position, no. 3, accuracy of identification in first visits was reduced from 60 to 35 per cent, and many more exploratory visits were required to locate the correct feeder. These results show that the correct position of a food source can be learned fairly quickly and with reasonable accuracy without other clues, but that the additional clue of a distinctive color is a definite aid to accurate identification.

DISCUSSION

The results of this investigation show that Ruby-throated Hummingbirds are more strongly influenced by the location of a food source than by its color when offered a choice of different colored foods of the same quality. Once a food source has been located, color may then act as an important discriminator stimulus, but there is no evidence from this or other studies that hummingbirds have an innate or strongly developed preference for one color, including red.

Ruby-throated Hummingbirds that breed in the region where this study was conducted usually arrive on spring migration in the last week of May (Houston and Street 1959), a month or more before the flowering of plants. When they first arrive in the spring they have been observed to feed on sap from holes made by Yellow-bellied Sapsuckers (*Sphyrapicus varius*) and on spiders and other small arthropods on the branches and needles of spruce. Red is not a common flower among the plants of this region, and an innate preference for the color red might, therefore, be disadvantageous for these birds. A somewhat similar condition may exist for non-migratory hummingbirds in the tropics. Grant (1966) suggests that resident tropical hummingbirds live in an environment where there is a reasonably predictable food supply throughout the year, and that they could readily learn to locate food without the aid of a uniform flower color. In other words, a tendency to explore different food sources and the ability to use color as a discriminator stimulus in learning the location of a food source would be more adaptive than a fixed color preference.

Nevertheless, red is the predominant flower color among ornithophilous plants in some regions of the Nearctic, especially California and northwestern America. Grant (1966) has advanced a hypothesis relating the red coloration of ornithophilous plants to the migratory habits of the hummingbirds of these regions. She suggests that easy recognition of food sources by hummingbirds entering new feeding areas during migration is selectively advantageous for both the plants and their bird pollinators, and that the display of a common floral color by the different plant species in the area of migration would increase the probability of early recognition and subsequent identification. As red is complementary to green, it is a particularly conspicuous color during daylight hours against a background of natural vegetation, and is a good choice for a common flower color among ornithophilous plants. The results of this study do not confirm this hypothesis, but they provide data that substantiate the prevalence of feeding behaviors that are required by it.

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