EXPERIMENTS WITH ALLEN'S AND ANNA'S HUMMINGBIRDS AT SUGAR WATER FEEDERS IN SPRING

TONNA HARRIS-HALLER, Department of Biology, Texas A&M University, College Station, Texas 77840

STANLEY W. HARRIS, Department of Wildlife, Humboldt State University, Arcata, California 95521

Because most ornithophilous flowers in North America are red (Pickens, 1930, 1941, Pickens and Garrison 1931, Grant 1966, Grant and Grant 1968), a general belief has arisen that hummingbirds have coevolved an innate preference for red flowers. This view has been supported and challenged by field (Woods 1927, Wagner 1946, Stiles 1976) and experimental studies (Sherman 1913, Bené 1941, 1945, Lyerly et al. 1950, Collias and Collias 1968, Miller and Miller 1971, Ewald 1979, Wheeler 1980, Welker 1984). These and other workers have proposed that feeding hummingbirds may be influenced by weather, time of day, location of food source, chemical composition of nectar, concentration of nectar, proximity to perches, availability of alternate foods, and competition.

We recorded 7517 minutes of observations of Allen's (*Selasphorus sasin*) and Anna's (*Calypte anna*) hummingbirds at Arcata, Humboldt County, California, 20 February–3 May 1972 and 31 January–14 February 1973, using a station where experimental solutions could be presented to wild birds in a uniform, carefully controlled manner. At Arcata, Anna's Hummingbird, an uncommon resident, breeds in late winter and early spring. Allen's Hummingbird is a common to abundant spring migrant, summer resident, and breeder but occurs in winter only as a vagrant (Yocom and Harris 1975, Harris 1984). We recorded all *Selasphorus* as Allen's Hummingbird, but a few early spring migrants possibly were Rufous Hummingbirds (*S. rufus*), an uncommon spring migrant in northwest California (Yocom and Harris 1975).

METHODS

The experimental apparatus consisted of a piece of plywood approximately 1 m long, 75 mm wide, and 13 mm thick, nailed across the lower half of a sash window of a suburban residence. The board was held about 100 mm from the glass. The window was adjacent to a larger window on one side and a blank wall on the other side. We drilled four holes, 200 mm apart, in the board. Experimental solutions consisted of ordinary white sugar (sucrose) and water in 61-ml feeders. Each feeder consisted of a clear glass bottle and a clear glass stem (feeder tube) held in the bottle by a small red rubber cork. In most experiments, we covered the red corks with white plastic tape. We discarded red plastic support sleeves supplied with the feeders. The stem of each feeder was inserted through a hole in the board, and the feeder was held in place with white elastic tape. We used four feeders in 1972, but in 1973 we placed feeders only in the two center holes of the board. We rotated the feeders across the positions on the board daily;

thus, each experimental solution occupied each position once every four days in 1972 and every other day in 1973. Feeder position 1 was closest to the adjacent window and position 4 was adjacent to the blank wall. We refilled feeders with experimental solutions at the end of each day's activity or more often as needed. We determined the initial positions of feeders by throwing a die. We separated some experiments with "rest" periods 3–24 days long, when we replaced experimental feeders with a large feeder hung in front of the board to maintain the interest of the birds in the station. The large feeder was filled with colorless 50 percent sugar water.

We measured hummingbird use of the station in three ways: (1) The appearance of one bird hovering or perching immediately in front of a feeder was scored as a "visit" with each shift of a bird between feeders scored separately. Birds appearing at the station simultaneously were all scored separately. (2) The act of a bird inserting its bill into the stem of a feeder was scored as a "sip" regardless of the duration of each sip. A single visit might generate 0 to 30+ sips. (3) Total daily consumption at each feeder was measured with a graduated cylinder when the feeders were refilled to maximum capacity. We abandoned attempts to record the duration of visits and sips with a stopwatch because we were unable to record data fast enough when spring migrants sometimes made more than 30 visits per minute and when two to seven birds commonly made simultaneous visits.

We recorded data from inside the house through a closed window. Window shades covered the top half of the window supporting the feeder rack and all of the large window immediately adjacent to feeder position 1. We took records sporadically throughout many days, but most data were from the two hours before and the one-half hour after sunset. We recorded the species and sex of each visitor.

We conducted experiments to test (1) sugar concentration preference, (2) feeder position preference, (3) red–blue–yellow–green color preference, (4) red–blue color preference, and (5) the effect of adding a perch on use rates of feeders. Protocols for each experiment were as follows:

Concentration trials—Trial 1: 20–26 February 1972, 1590 minutes of observation time. Trial 2: 27 February–5 March 1972, 1371 minutes. Experimental solutions: 0 (plain water); 33% sugar (one part sugar to two parts water by volume); 50% sugar (equal parts sugar and water by volume); 66% sugar (two parts sugar to one part water by volume). All solutions and feeders were uncolored, feeders were rotated for position daily, and stem corks were covered with white plastic tape.

Position trial—8–14 March 1972, 1919 minutes. All feeders contained colorless 50% sugar solution, were uncolored, were rotated daily, and had their stem corks covered with white plastic tape.

Color trial 1—16–23 March 1972, 1132 minutes. All feeders contained colorless 50% solution and were rotated daily. The entire feeder, including stem, stem cork, and bottle, was wrapped with colored plastic tape to achieve clear, consistent colors that could be duplicated without introducing any taste bias that might happen with food dyes. Colors used were red, blue, yellow, and green.

Color trial 2—31 January–14 February 1973, 803 minutes. Protocol as above except we used only red and blue feeders and rotated these on alternate days between the two center positions on the board.

Perch trials—17–24 April 1972 and 26 April–3 May 1972, 712 minutes. We attached a movable wire perch in front of one feeder. This perch was rotated across the board between the positions daily. Feeders were uncolored and filled with colorless 50% sugar water; red stem corks were exposed. We measured use in the first trial by visits, sips, and total consumption, in the second trial by total consumption only.

In most experiments, we tested the results with a chi square analysis using pooled data for each experiment (d.f. = 1) and the hypothesis that the expected rates of use for any single feeder equaled 25% (1:3 ratio) of total use in the four-feeder, 1972 trials, and 50% (1:1 ratio) of total use in the two-feeder, 1973 trials.

RESULTS

Seasonal and Species Composition of Use

Between 31 January and 14 February 1973, we recorded only Anna's Hummingbirds during 803 minutes of observations. This species made 31.4 visits per 100 minutes of observation time, nearly 92% by males (Table 1). Between 20 February and 26 February 1972, Allen's Hummingbirds accounted for 26% of all visits, but no females of either species were seen (Table 1). By late February and early March, the proportion of Allen's Hummingbirds had increased to about one-third of all visits, and the rate of visits per 100 minutes of observation time had increased, but no females had yet appeared. In the second week of March, female Allen's Hummingbirds appeared at the feeders as frequently as males, while use rates of Anna's Hummingbird males remained essentially unchanged from the previous period. By late March, use rates by Allen's increased to more than 60 visits per 100 minutes for each sex, while the use by Anna's males remained stable at about 34 visits per 100 minutes (Table 1). By mid-April, use by both sexes of Allen's and by male Anna's had increased dramatically. A striking aspect of these data is that female Anna's Hummingbirds rarely used the station, though they occasionally foraged in nearby flower beds.

Simultaneous Visits

Of 1082 total visits recorded in early trials (31 January–5 March), 99.8% involved single birds. The frequency of simultaneous visits increased with the influx of spring migrants to 16.5% of 2461 visits (8–14 March) and 35.1% of 4228 visits (16–24 March). Simultaneous visitors either shared a feeder and drank at the same feeder stem, or they made unshared visits to different feeders on the rack. All data combined, 81.1% of 7773 visits were by single birds, 13.8% were by two or more birds feeding simultaneously at different feeders, and 5.1% were of two or more birds sharing one feeder. Nearly two-thirds (64.7%) of the 1472 birds recorded feeding together occurred as pairs, another 357 (24.3%) occurred in groups of three, 124 (9.4%) occurred in groups of four, and 39 (2.5%) in groups of five or more.

Table 1 Seasonal Distribution of Rate and Percentage of Visits at Sugar-Water Feeding Station by Allen's and Anna's Hummingbirds, Arcata, Humboldt County, California

		Allen's Hummingbird				Anna's Hummingbird			
		Males		Females		Males		Females	
Period	Type of Trial	Visits/ 100 min	Percent Total	Visits/ 100 min	Percent Total	Visits/ 100 min	Percent Total	Visits/ 100 min	Percent Total
31 Jan–14 Feb 1973	Color 2	0	0	0	0	28.8	91.7	2.6	8.3
20–26 Feb 1972	Concentration 1	4.3	26.1	0	0	12.2	73.9	0	0
27 Feb–5 Mar 1972	Concentration 2	13.0	31.0	0	0	28.9	69.0	0	0
8–14 Mar 1972	Position	48.4	37.7	46.3	36.2	33.2	25.9	0.25	0.2
16–23 Mar 1972	Color 1	60.4	37.5	65.7	40.8	34.2	21.2	0.8	0.5
17–24 Apr 1972	Perch 1	80.5	23.8	199.7	59.1	57.3	17.0	0.2	0.1

The largest single group we saw was seven birds at four feeders simultaneously during the position trial and the largest number we saw sharing a single feeder was four at a red feeder during the first color trial.

Concentration Trials

In the first concentration trial, both species preferred the 50% solution as measured by both visits and sips. Both species generally visited the 66% solution at about the expected rate (Table 2), but Anna's exceeded the expected rate when measured by sips. Both species generally used the clear water and 33% solutions at less than expected rates. The total consumption of sugar water by both species combined deviated from the expected 25% rate for clear water (no measurable amount taken) and the 66% solution (50% of all sugar water taken).

In the second trial, both species avoided the clear water and preferred the 66% solution. Allen's Hummingbirds used the 33 and 50% solutions at about expected rates, but Anna's Hummingbird used the 50% solution at greater than expected rates and the 33% solution at less than expected rates.

Effect of Feeder Position

We conducted the position trials after many female Allen's Hummingbirds had joined the feeding flock (Table 1). Both sexes of Allen's Hummingbird generally used position 1 at less than expected rates as measured by visits (13.4% of 928 visits by males, 16.4% of 890 visits by females) and

Table 2 Percentage of Use of Four Concentrations of Sugar Water by Male Allen's and Anna's Hummingbirds, 20 Feb–5 Mar 1972, Arcata, Humboldt County, California

Species	Measure of Use	*n*	Percentage of Sugar 0	33	50	66
Trial 1 (20–26 Feb 1972)						
Allen's	Visits	67	6.0[a]	17.9[b]	55.2[a]	20.9[b]
	Sips	288	2.0[a]	10.8[a]	61.5[a]	25.7[b]
Anna's	Visits	194	6.7[a]	15.4[a]	47.9[a]	29.0[b]
	Sips	1350	1.1[a]	14.1[a]	46.5[a]	38.2[a]
Total Consumption (ml)		60	0[a]	16.7[b]	33.3[b]	50.0[a]
Trial 2 (27 Feb–5 Mar 1972)						
Allen's	Visits	177	4.5[a]	22.0[b]	31.6[c]	41.8[a]
	Sips	629	1.2[a]	21.8[b]	28.0[b]	49.0[a]
Anna's	Visits	394	4.3[a]	13.7[a]	34.5[a]	47.4[a]
	Sips	1727	1.3[a]	7.3[a]	33.6[a]	57.8[a]

[a]$P < 0.01$. P based on χ^2 from pooled data for all days of observation (d.f. = 1); χ^2 hypothesis is that expected rate of use for any single concentration = 25% of total.
[b]Not significant.
[c]$P < 0.05$.

sips (15.7% of 2144 sips by males, 17.3% of 2440 sips by females; $P <$ 0.01 for all tests). Male Allen's used positions 3 (31.5% of visits, 32% of sips) and 4 (28.7% of visits, 29.3% of sips) at greater than expected rates, but female Allen's exceeded expected rates (33.7% of visits, 33.1% of sips; $P < 0.01$ for all tests) only at position 4. Male Anna's exceeded expected rates at position 2 (29% of 638 visits and 28% of 1903 sips, $P < 0.02$ for visits and < 0.01 for sips), and visited position 3 at a less-than-expected rate (21.2%; $P < 0.01$) as measured by sips. As measured by consumption, the amount of total solution taken at position 1 was slightly less (20.9% of 401 ml) than at the other positions, but this difference was not strongly significant ($P < 0.10$). To summarize, there was a bias by Allen's Hummingbird away from the feeder nearest the adjacent window (position 1) and toward the feeder nearest the blank wall (position 4, but Anna's Hummingbird did not show a strong bias for or away from any feeder position.

Color Trials

In 1972 male Allen's and Anna's and female Allen's hummingbirds all used the red feeder at rates higher than expected as measured by visits, sips, and total consumption (Table 3). Though the sample for female Anna's Hummingbirds was too small to test statistically, 55.5% of all visits and 69% of all sips recorded were at the red feeder, compared to expected rates of 25%. Male Allen's also used the blue feeder more than expected as measured by both visits and sips, but the female Allen's used the blue feeder less than expected. Both sexes of Allen's Hummingbird used the yellow and green feeders less than expected with the green feeder the least preferred by far. Male Anna's Hummingbird used the green feeder far less than expected and generally used the blue and yellow feeders about as expected.

Table 3 Percentage of Use of Sugar-Water Feeders of Four Colors by Allen's and Anna's Hummingbirds, 16–23 Mar 1972, Arcata, Humboldt County, California

Species	Sex	Measure of Use	*n*	Color: Red	Blue	Yellow	Green
Allen's	Male	Visits	684	44.4[a]	31.1[a]	13.9[a]	10.5[a]
		Sips	1757	47.2[a]	28.2[a]	14.2[a]	10.4[a]
Allen's	Female	Visits	744	62.6[a]	19.2[a]	13.4[a]	4.7[a]
		Sips	2305	66.4[a]	19.3[a]	10.1[a]	4.1[a]
Anna's	Male	Visits	388	38.4[a]	24.2[b]	22.7[b]	14.7[a]
		Sips	1454	35.7[a]	23.4[b]	28.5[a]	12.5[a]
Anna's	Female	Visits	9	55.5[c]	0[c]	33.3[c]	11.1[c]
		Sips	29	69.0[c]	0[c]	24.1[c]	6.9[c]
Total Consumption		(ml)	367	61.6[a]	17.8[a]	13.8[a]	6.9[a]

[a]$P < 0.01$. P based on χ^2 values from pooled data for all days of observation (d.f. = 1); χ^2 hypothesis is that expected rates of use for any single color = 25% of total.
[b]Not significant.
[c]Sample size for female Anna's Hummingbird too small to calculate χ^2 values.

These birds consumed 61.6% of all sugar water taken through the red feeder, a rate much greater than expected, and they took nectar from the other three colors at rates less than expected. The least used feeder was green, accounting for only 6.9% of the total consumption during the 8-day trial.

Further clear evidence of the preference for the red feeder is demonstrated by data on simultaneous visits. Birds arriving at the station when another bird was already present were confronted with four choices: (1) displace the bird already present and take over its feeder; (2) share the same feeder with the first bird; (3) use a nearby or adjacent feeder and drink there simultaneously; or (4) leave without drinking. We observed all four events frequently. All data combined, about 50% of all single visits were at the red feeder, 40.3% of birds feeding simultaneously but at separate feeders used the red feeder, and 75.7% of birds sharing the same feeder were at the red feeder. In fact, of all trials, the highest rate of shared use occurred during the color trial when 9.7% of 1825 visits were shared visits compared to only 5.9% for the perch trial (2403 visits) and only 2.7% for the position trial (2461 visits). During the color trial, most birds sharing a single feeder were at the red feeder. In some cases a bird originally using the red feeder was displaced by an arrival only to move to another color when the arrival took over the red feeder; in these cases, it was clear that the first color of choice for both birds was red.

We offered red and blue in early February 1973 when only Anna's Hummingbird was present (Table 1). Male Anna's used the red feeder at rates much higher than expected as measured by both visits and sips (Table 4). Female Anna's also used the red feeder more than the blue feeder, but the difference was not significant for the small sample of observations (Table 4). Nearly 71% of all sugar water taken in the trial was from the red feeder compared to an expected 50%.

Table 4 Percentage of Use of Sugar-Water Feeders of Two Colors by Anna's Hummingbirds, 31 Jan–14 Feb 1973, Arcata, Humboldt County, California

Sex	Measure of Use	*n*	Percent Total Use	
			Red	Blue
Male	Visits	231	62.8	37.2[a]
	Sips	833	65.4	34.6[a]
Female	Visits	21	57.1	42.9[b]
	Sips	42	64.3	35.7[b]
Total Consumption (ml)		236	70.8	29.2[a]

[a] $P < 0.01$. P based on χ^2 values from pooled data for all days of observation (d.f. = 1); χ^2 hypothesis is that expected rate of use of any single color = 50%.

[b] Not significant.

Perch Trials

Male Allen's Hummingbird visited feeders with a perch on 18.5% of 573 visits, less than the expected 25% rate ($P < 0.01$), but female Allen's and male Anna's showed no preference for or against the perch. Female Allen's and male Anna's sipped from feeders with a perch more than expected (33.9% of 4031 sips and 36.7% of 1492 sips, respectively, $P < 0.01$), but male Allen's did not. In both trials total consumption at feeders with perches exceeded expected rates ($P < 0.01$)

Daily Pattern of Use

Rates of use were at generally low levels for both species most of the day, but increased dramatically beginning about 1700 hours and continued to increase until feeding activities stopped 30–45 minutes after local sunset (Figure 1). Generally any territorial claims established during the day were overwhelmed near sunset when many birds appeared and when some individuals, particularly male Anna's, made visits consisting of 20+ sips

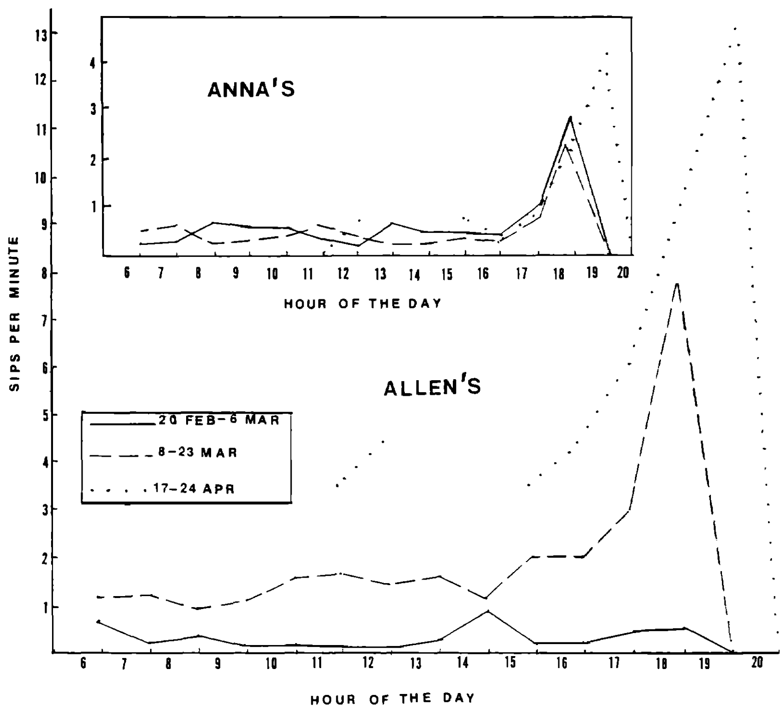

Figure 1. Hourly distribution of feeding activity at sugar water feeders by Allen's and Anna's hummingbirds, spring 1972, Arcata, California.

compared to an average of 2–3 sips per visit during other daylight hours. This pattern of increased use late in the day remained constant throughout the spring.

DISCUSSION

The 1972 studies occurred during a spring of unusually heavy use. Observations in other years suggest that "normal" usage rates in March and April were about one-quarter as high as in 1972. We have no explanation for the heavy use in 1972, but migrant swarms of hummingbirds sometimes are attracted to seasonal food sources (Stott 1942, Stiles and Wolf 1970). Our data showed that male Allen's Hummingbirds migrate into California's north coast somewhat earlier than do females. Phillips (1975) reported a similar pattern in both spring and fall.

Female Anna's Hummingbirds used the station only slightly. Possible explanations could be a low population of females in the area during the study, varying nutritional requirements for females just entering the nesting period (Pitelka 1951, Kelly 1955), or the inability of females to compete with massive numbers of migrant Allen's and the normal territoriality of male Anna's Hummingbirds. Most of the recorded usage by female Anna's was in February 1973, before any Allen's arrived. Even then, males outnumbered females (Table 1). Several workers have mentioned that female hummingbirds do not feed in males' territories and defend only small territories near the nest while breeding. Southwick and Southwick (1980) reported that female Ruby-throated Hummingbirds (*Archilochus colubris*) fed solely on tree sap at sapsucker holes in Michigan in early spring, while males used both nectar and sap. Ewald (1979) found that female Anna's were less territorial and less able than males to defend food sources. Nesting female Costa's Hummingbirds (*Calypte costae*) seemed to visit flowers less often than did males, but foraged inside nonflowering trees and shrubs (Woods 1927). Similar patterns have been reported for tropical species (Stiles and Wolf 1970). Male White-eared Hummingbirds (*Hylocharis leucotis*) excluded females and immatures from the "most suitable" flowers and forced them to feed at flowers under vegetative cover (DesGranges 1978).

Our study was conducted at a time when when Anna's Hummingbird apparently was in the process of colonizing the north coast as a nesting species (Zimmerman 1973), and it is possible that the early invaders in the range extension process were mostly males. Anna's Hummingbird is now an established breeder in the area, yet we still rarely see females at sugar water feeders.

Previous workers have emphasized the importance of the relative position of food sources and of perches as a factor determining hummingbird food use (Bené 1945, Collias and Collias 1968, Miller and Miller 1971, Wheeler 1980). In our study, Allen's Hummingbirds used feeder position 1 at less and feeder position 4 at more than expected rates even though all feeders were essentially equidistant from perches used by the birds. Feeder 1 was adjacent to a large window that opened into the same room as the experimental window, and human activity inside the room may have influenced the use of that feeder even though we kept the shade drawn during observation sessions. Conversely, position 4 was adjacent to about 3 meters of blank wall and was the farthest removed from any activity visible through the window. Welker (1984) reported that Anna's Hummingbird preferred the two end positions at a station were four feeders were arranged in a linear fashion similar to ours. In our study, male Anna's did not show any strong preference for any of the four feeder positions. It is possible that use by Allen's Hummingbirds of certain feeders may have influenced Anna's to use other, open feeders, but data on simultaneous use showed that, during the position trial, nearly 84% of 2054 visits were of single birds with a free choice of any feeder position. Thus, it seems unlikely that any detectable interspecific competitive exclusion occurred.

Our protocols called for a regular rotation of each experimental solution through all four positions in an effort to minimize any tendency to a position bias. Most trials lasted for 8 days, and each experimental solution was thus exposed to two complete rotations of the positions. Furthermore, the results of each experiment were pooled for all 8 days before analysis, thus further minimizing any position bias.

Van Riper (1958) found that Broad-tailed Hummingbirds (*Selasphorus platycercus*) in Colorado preferred sucrose over five other sweeteners, and a 50% sugar solution over weaker ones. Collias and Collias (1968) failed to get Anna's Hummingbird to use solutions with lower than 1:8 dilution ratios. In our concentration trials, both species quickly discriminated the plain-water feeder. The only visits/sips made at plain water were quick exploratory tests that, once made, did not seem to be repeated until the feeder position was changed the next day. The ability of birds to remember which of four identical feeders was unproductive and to avoid it maximizes the energetic efficiency of foraging. That the birds preferred the 50 and 66% solutions over weaker ones is clear evidence of their ability to seek rich nectar sources, with obvious survival value (Hainsworth and Wolf 1976). Even the 33% solution exceeded the apparent concentration of most natural floral nectar (Wagner 1946, Baker 1975, Stiles 1976, Hainsworth 1981, Tyrrell 1985).

The main effect of adding a perch to the feeders was to reduce the number of visits made by male Allen's and to increase the number of sips made by female Allen's and male Anna's over expected rates. Generally, the perch allowed an individual to defend a feeder more securely than when it had to hover. Thus, visits were longer, reducing the total number of visits possible at a feeder in a given time, but increasing the number of sips and the total consumption at feeders with perches. Additionally, male Allen's took 2.3 sips per visit without the perch compared to 3.7 with the perch; female Allen's took 2.5 without and 4.0 with, and male Anna's took 3.0 without and 5.7 with the perch. Though the results are mixed and not strongly conclusive statistically, the perch apparently made the feeder generally more efficient for the birds to use.

Some workers have found early morning (Stiles and Wolf 1970) or evening (DesGranges 1978) peaks in feeding rates, while others found no diurnal patterns (Wolf and Hainsworth 1977, DesGranges 1978). One might expect birds to seek reliable, known food sources actively at the beginning of the day after a long night's fast, but neither of our species showed this pattern. The visitation rate for either species did not change from dawn until the last 1 to 2 hours before sunset, when visitation and sip rates for both species increased greatly.

The heavy use at the end of the day probably represents a need for the birds to take one last heavy energy load before the long night's inactivity. Territorial claims disintegrated during the last 90 minutes of activity and many simultaneous visits were recorded then. Also, birds often made long, 20- or 30-sip visits at that time, compared to 1- to 3-sip visits earlier in the day.

The most striking result of our studies is the clear, strong preference for the red feeder when a choice of red, blue, yellow, and green was offerred. Blue was a poor second choice, and green was by far the least preferred color of those offered. The effect was somewhat stronger for Allen's Hummingbird than for Anna's, but the results for both were highly significant. Welker (1984) worked with Anna's Hummingbirds in fall and winter in northwestern California and reported results exactly opposite to ours. She found green most and red least preferred and suggested a possible seasonal explanation for the difference. Our 1973 mid-winter results also showed a clear preference for red, but we did not offer green in that experiment. Welker's (pers. comm.) experimental apparatus and hence her results are not directly comparable to ours. She retained the plastic red sleeves supplied with the feeders as a means of hanging them. Consequently her feeders all had about one-quarter to one-third of the bottle covered with a red band that was visible to a feeding or hovering bird in spite of the fact that she placed over each feeder a hood made of construction paper of a color to match her experimental solutions. Also, she did not cover the small red corks that held the feeder stems in the bottles so that all of her feeders had red visible in two places, in addition to her colored solutions. Michael Hansen (pers. comm.) conducted a study similar to ours in the same area in a later spring and offered red, pink, white, and yellow. He found that Allen's, Rufous, and Anna's hummingbirds all preferred red over the other colors with pink a second choice and white a poor third. Pickens (1930, 1941) and Pickens and Garrison (1931) suggested that hummingbirds prefer red or violet colors, but their conclusions were not based on extensive carefully controlled experiments. Wheeler (1980) found red preferred in a well-controlled experiment, as did Collias and Collias (1968) for one female Anna's Hummingbird but not for others. Bené (1941), in a short-term, poorly controlled study, found that male Black-chinned Hummingbirds (*Archilochus alexandri*) males preferred yellow and females preferred colorless feeders. Later, Bené (1945) failed to show any clear preference for color by Black-chinned Hummingbirds. Miller and Miller (1971) also failed to show a strong preference for color in a reasonably well-controlled experiment, as did Lyerly et al. (1950).

Whether color preference is learned or innate cannot be determined from the data generated by this study, but it seems likely that hummingbirds learn to perceive color, especially red, to locate likely food sources. It is also likely that there has been a degree of coevolution between the development of red-flowered ornithophilous plants in western North America (Grant

1966) and the use of color vision by hummingbirds while foraging. Because red flowers stand out against natural green backgrounds (Grant 1966) and red is not often detected by insects, particularly bees (Raven 1972), it would be mutually advantageous for birds to develop a red color sense and for plants with bird-pollinated flowers to develop red flowers. Red would advertise nectar locations that birds learn, from an early age, to recognize as food sources (Stiles 1976). It is likely our birds already had learned to associate artificial feeders with red before these studies began. Virtually every feeder in California either uses red solution or has red-colored plastic as part of its construction. At the time of these studies, other nearby residences had operating feeders and all presented red liquid. Such preconditioning probably influenced the birds to use red when they arrived at our experimental station. Indeed, it may not be possible to find spring migrant hummingbirds in California that have not already been preconditioned to red artificial feeders!

Because high rates of use were obtained without bright colors in some of our trials, these birds obviously use other clues to find food. They undoubtedly learn where food sources are by watching other birds, and they certainly investigate any brightly colored object while foraging. We once watched a male Anna's move, in mid-winter, systematically down a line of colored Christmas lights along the eave of a house. The bird poked at each bulb regardless of color before moving to the next. The bulbs were red, blue, yellow, white, orange, and green and all were tested. During the perch trial, the red corks were left exposed and represented the only patches of bright color at the station. Apparent new arrivals invariably poked at each red cork in turn several times before learning they had to sip at the end of the feeder stem about 40 to 50 mm away. A male Calliope Hummingbird (*Stellula calliope*), a rare migrant in the area, came to the station, poked at each red cork in turn and flew off without feeding. Five minutes later he repeated the process.

Hummingbirds can use colors other than red as a "flag." Wagner (1946) found that hummingbirds in a controlled experiment took colors matching those of natural flowers most frequently visited in the same season. Stiles (1976), working with recent captives, suggested the same conclusion. Collias and Collias (1968) reported that birds tended to persist using a color once it had been identified as a food source. In carefully controlled experiments, Stiles (1976) ranked the most important factors determining use: (1) concentration of nectar, (the sweeter, the better), (2) taste (sucrose best), (3) color. He suggested that color conditioning may operate as an orientation stimulus and that red would be the best color for advertising. Woods (1927), Miller and Miller (1971), and Wheeler (1980) all concluded that location of a source, once identified as food, was more important than color in continued use of the source. It is clear that hummingbirds can remember the locations of food sources (Bene 1945, Ewald 1979) for days or even months.

We conclude that Allen's and Anna's hummingbirds make use of color vision and that discrimination of red is an important, though not indispensable, tool these birds use while foraging. Once a source is found, it is likely that other factors such as memory of location, availability of perches, competition, quality and quantity of available nectar, etc., may be equally or more important than color in continued use of the source. The use of color in the initial location of food sources is aided by an apparent insatiable curiosity of hummingbirds to investigate all bright or unusual objects in their environment.

We are indebted to Dr. David Kitchen and Dr. Tim Manolis for critically reviewing the manuscript and making many useful suggestions for improvement.

LITERATURE CITED

Baker, H. G. 1975. Sugar concentrations in nectars from hummingbird flowers. Biotropica 7:37–41.

Bené, F. 1941. Experiments on the color preference of Black-chinned Hummingbirds. Condor 43:237–242.

Bené, F. 1945. The role of learning in the feeding behavior of Black-chinned Hummingbirds. Condor 47:3–21.

Collias, N. E., and Collias, E. C. 1968. Anna's Hummingbirds trained to select different colors in feeding. Condor 70:273–274.

DesGranges, J. L. 1978. Organization of a tropical nectar feeding bird guild in a variable environment. Living Bird 17:199–236.

Ewald, P. W. 1979. The hummingbird and the calorie. Nat. Hist. 88(7):92–98.

Grant, K. A. 1966. A hypothesis concerning the red coloration in California hummingbird flowers. Am. Nat. 100:85–97.

Grant, K. A., and Grant, V. 1968. Hummingbirds and Their Flowers. Columbia Univ. Press, New York.

Hainsworth, F. R. 1981. Energy regulation in hummingbirds. Am. Sci. 69:420–429.

Hainsworth, F. R., and Wolf, L. L. 1976. Nectar characteristics and food selection by hummingbirds. Oecologia 25:101–113.

Harris, S. W. 1984. Field Checklist of Northwest California Birds. Redwood Region Audubon Soc., Eureka.

Kelly, J. W. 1955. History of the nesting of an Anna's Hummingbird. Condor 57:347–353.

Lyerly, S. B., Riess, B. F., and Ross, S. 1950. Color preference in the Mexican Violet-eared Hummingbird, *Colibri t. thalassinus* (Swainson). Behavior 2:237–248.

Miller, R. S., and Miller, R. E. 1971. Feeding activity and color preference of Ruby-throated Hummingbirds. Condor 73:309–313.

Phillips, A. R. 1975. The migrations of Allen's and other hummingbirds. Condor 77:196–205.

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

Pickens, A. L. 1941. A red figwort as the ideal Nearctic bird flower. Condor 43:100–102.

Pickens, A. L., and Garrison, L. P. 1931. Two-year records of the Ruby-throat's visit to a garden. Auk 48:532–537.

Pitelka, F. 1951. Breeding seasons of hummingbirds near Santa Barbara, California. Condor 53:198–201.

Raven, P. H. 1972. Why are bird-visited flowers predominantly red? Evolution 26:674.

Sherman, A. R. 1913. Experiments in feeding hummingbirds during seven summers. Wilson Bull. 25:153–166.

Southwick, E. E., and Southwick, A. K. 1980. Energetics of feeding on tree sap by Ruby-throated Hummingbirds in Michigan. Am. Midland Nat. 104:328–334.

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

Stiles, F. G. and Wolf, L. L. 1970. Hummingbird territoriality at a tropical flowering tree. Auk 87:467–491.

Stott, K. Jr. 1942. An unusual concentration of hummingbirds. Condor 44:282.

Tyrrell, E. Q. 1985. Hummingbirds: Their Life and Behavior. Crown, New York.

Van Riper, W. 1958. Hummingbird feeding preferences. Auk 75:100–101.

Wagner, H. O. 1946. Food and feeding habits of Mexican hummingbirds. Wilson Bull. 58:69–93.

Welker, H. J. 1984. Food color preference in the Anna's Hummingbird. W. Birds 15:23–27.

Wheeler, T. G. 1980. Experiments in feeding behavior of the Anna's Hummingbird. Wilson Bull. 92:53–62.

Wolf, L. L., and Hainsworth, F. R. 1977. Temporal patterning of feeding by hummingbirds. Animal Behavior 25:976–989.

Woods, R. S. 1927. The hummingbirds of California. Auk 44:297–318.

Yocom, C. F., and Harris, S. W. 1975. Birds of Northwestern California. Humboldt State Univ. Bookstore, Arcata, CA.

Zimmerman, D. A. 1973. Range expansion of Anna's Hummingbird. Am. Birds 27:827–835.

Accepted 24 April 1991