TASTE PREFERENCES, COLOR PREFERENCES, AND FLOWER CHOICE IN HUMMINGBIRDS

F. GARY STILES

Taste and color preferences have been experimentally demonstrated for a variety of birds, and the literature on food habits of wild birds is enormous, but as yet there is little to tie the two together. Laboratory experiments have usually involved taste stimuli that are probably irrelevant to birds in the wild; and the taste stimuli presented by insects, seeds, fruit, etc. are complex and difficult to duplicate for experimental purposes. The same is true to a considerable extent of color: the mostly granivorous species studied so far probably never experience bright, monochromatic colors in connection with feeding. Moreover, caloric parameters of birds' foods are often difficult to measure or estimate but will almost certainly affect food selection, making taste and color preferences harder to assess.

Hummingbirds are ideal subjects in studies of taste and color preferences. Their main foods are nectar and insects; flowers are visited almost exclusively for nectar, insects being captured elsewhere. Flower nectar is essentially an aqueous solution of 3 common sugars (Percival 1961, see also beyond). It can be easily sampled and its concentration, caloric value, and composition measured. The taste stimuli can be readily duplicated and manipulated experimentally. Assimilation of flower nectar is essentially 100% (Hainsworth 1974) making caloric parameters easy to estimate. Flowers visited by hummingbirds are usually brightly colored and fairly unpatterned, also favoring experimentation.

The long controversy over the existence of color preferences in hummingbirds was reviewed by Grant and Grant (1968). The roles of color and taste factors have been greatly clarified by the feeding station experiments of Collias and Collias (1968); similar experiments by Miller and Miller (1971) further elucidated the role of position. These studies suggest a hierarchy of factors influencing feeder choice: sugar concentration and/or taste over position over color. As yet this hierarchy has not been subjected to experimental verification, or applied in detail to flower choice in the field.

This paper presents laboratory experiments on taste and color preferences of the Anna Hummingbird (*Calypte anna*) and several other species. I also present the results of extensive field observations on flower choice by hummingbirds, and consider the taste and color stimuli presented by those flowers visited by hummingbirds. Hopefully, comparing the results of field and laboratory studies will permit a more realistic evaluation of the role of taste and color preferences in food choice by hummingbirds, and a better understanding of the coevolution of hummingbirds and the flowers they pollinate.

LABORATORY EXPERIMENTS ON TASTE AND COLOR PREFERENCES

The laboratory experiments reported here were carried out at the University of California, Los Angeles, between spring 1966 and fall 1969. Hummingbirds were captured with mist nets, either at wild or cultivated flowers, or at feeding stations. They were transferred to the laboratory in a carrying case as described by Lasiewski (1962). When not being used in experiments, birds were housed in groups of 4 to 8 in holding cages 50 × 50 × 100 cm in size. In general, a large number of birds and a small number of feeders prevented domination of the feeders by one or two birds, and insured that birds low in the cage dominance hierarchy were able to feed.

The experimental cage was cubical, 50 cm on a side, containing a central perch and 2 to 4 feeders, depending on the experiment. The cages were designed to minimize position variables by placing the feeders close together and equidistant from the perch. The feeders were inverted 25- or 50-ml polystyrene graduated cylinders with a glass tube and rubber cork inserted in the open end. Cages were lighted by fluorescent lamps emitting light of approximately the same spectral composition as sunlight. The birds were kept on a 12-hr photoperiod in a windowless room; temperature fluctuated between 17 and 22°C.

The sugars used in all experiments were sucrose, glucose, and fructose, and various mixtures thereof; these sugars are the main constituents of flower nectars (Percival 1961). Sugar solutions were made up on a weight sugar per volume solution basis, with concentrations expressed as percentages (e.g. 30% = 30 g sugar in 100 ml solution). Percentage, rather than molarity, was used because the disaccharide sucrose has a molecular weight approximately twice that of the monosaccharides glucose and fructose, but the number of calories per gram is nearly the same for all 3 sugars. For color preference experiments, colored disks approximately 2 cm in diameter were affixed to the mouths of the feeder tubes. The colors used were made up by mixing acrylic paints to obtain as nearly equal brightness as possible. Brightness was assessed as percentage of incident light reflected at the wavelength of maximum reflectance, by a Beckman G2 spectrophotometer fitted with a reflectance unit (see Porter 1967, for a detailed description of

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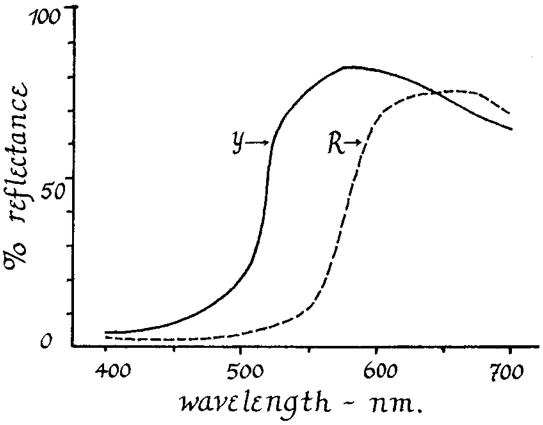

FIGURE 1. Spectral reflectance curves of red and yellow paints used in color preference experiments.

this apparatus). Figure 1 gives spectral reflectance curves for red and yellow paint mixtures used in the experiments described below.

Besides the sugar solutions, birds were given fruit flies (*Drosophila*) daily. As my *Drosophila* colony was of small and variable size, the number of flies given varied considerably; this probably accounts for much of the daily variation in sugar consumption observed in many of the experiments. At approximately weekly intervals (except during experiments) a protein-vitamin mixture (cf. Lasiewski 1962) was substituted for the sugar solutions for one day. I found that hummingbirds could be maintained for at least 1 year on these rations, although mortality in captive birds averaged about 2–5% per month.

When newly-captured birds were first brought into the lab, they consumed food at a high rate and gained weight. Then, over a period of several weeks, birds consumed less food and lost weight, finally levelling off at 80–90% of their weight at capture. This pattern was probably due to an overall reduction in activity of captive birds, who flew for about 10% of the time. In the wild, male Anna Hummingbirds spend about twice as much time flying (Pearson 1954, Stiles 1971). Since the "nights" indoors were no colder than the days, birds may not have maintained the same level of fat reserves against the nocturnal fast in the laboratory, accounting for their lower equilibrium weight there (cf. Hartman and Brownell 1959).

During each of the experiments, a given feeder arrangement was maintained for 24 hr (12 hr of activity by the birds). Feeders were changed at approximately the same time each day. This gave the bird plenty of time to sample all feeders, thereby hopefully minimizing position effects. Preferences were measured as the amounts of sugar consumed out of different feeders over the course of the experimental period. I noticed that birds would often visit the feeder in the position of the previous day's preferred solution for the first hour or two before visiting the other feeder(s) and perhaps changing their preference. Position of the feeders was determined daily by coin flip or random number table. Loss of solutions through evaporation or dripping was negligible in all experiments reported here.

In interpreting the experimental results, I have been mainly interested in the overall reactions of groups of birds, rather than individual variation within groups. However, I have consistently analyzed for individual variation by chi-square tests, and have noted significant intragroup heterogeneity where it occurs. In such cases, any conclusions based on the group totals should be treated with appropriate reservations. In a bird-flower interaction, selection pressures are exerted on the plant population as a whole by the bird population as a whole, and vice versa: it is the resultant of the individual variation that is important at the population level!

Details of procedure and results will be considered for each experiment in turn below. Not all birds in an experiment were run simultaneously, and experiments were not necessarily run in the order presented here, due largely to the unpredictability in capturing new birds.

EXPERIMENTS

EXPERIMENT 1

Do Anna Hummingbirds prefer certain sugars when brought into the laboratory?

Procedure: Four experimental 30% sugar solutions (sucrose, glucose, fructose, and mixture of equal parts of all 3) were presented in pairs; each bird was given each possible combination of two sugars on two separate days. The birds used were 6 Anna Hummingbirds caught at feeders and 5 caught at flowers. Experiments were begun the day after the birds were brought into the lab.

Results: A similar order of preferences was found for both flower-caught and feeder-caught birds, but the preference for sucrose was slightly more marked in the latter (table 1). This suggests taste conditioning, since sucrose was used in the feeders. In general, individual differences in taste preferences are most pronounced in those sugar combinations where the total preference of the group is not

TABLE 1. Consumption of different 30% sugar solutions presented pairwise, by Anna Hummingbirds.

	Pairs of sugar solutions	S vs. F	S vs. G	S vs. M	G vs. F	G vs. M	F vs. M
6 birds caught at feeders	Amounts consumed (ml.)	115–25**	98–52**	78–41**	107–40**	77–85	32–103**
5 birds caught at flowers	Amounts consumed (ml.)	101–20**	(78–60)	(69–47)*	97–14**	(59–70)	16–89**

Abbreviations: S–sucrose; F–fructose; G–glucose; M–equal-parts mixture of all 3 sugars. Parentheses indicate significant individual variation as determined by chi-square test for heterogeneity. * = differential consumption significant at .05 level as determined by chi-square test; ** = significant at .01 level.

TABLE 2. Lengths of first feeding flight and weight changes of Anna Hummingbirds being given only sucrose or fructose, in relation to the sugar given on the previous day.

	Sugars			
	S following S	S following F	F following S	F following F
No. bird-days	15	35	30	15
Mean weight change (in gms/bird/day)	+0.03	+0.02	+0.02	–0.04
Range: weight changes	+0.2 to –0.2	+0.1 to –0.2	+0.3 to –0.2	+0.2 to –0.6
Mean length (sec) of first feeding flight	2.86	3.22	2.08	2.64
Range: length of first feeding flight	0.5 to 10.0	0.2 to 8.5	0.1 to 8.7	0.2 to 6.8

well marked. For instance, one of the flower-caught birds showed a slight preference for glucose over sucrose, and two preferred the mixture to sucrose. One flower-caught and two feeder-caught birds preferred glucose over the mixture. No bird preferred fructose in any combination. Thus, the overall preference of the two groups was sucrose over mixture over glucose over fructose, but the only unequivocal result for all birds was the rejection of fructose.

EXPERIMENT 2

If given no choice, will hummingbirds take a non-preferred sugar in the same amounts as a preferred one?

Procedure: This experiment involved 5 birds over a 20-day period. On any given day, a bird received 30% fructose or 30% sucrose; each bird received 10 days of each sugar over the course of the experiment. The order in which the sugars were given was determined by drawing an "S" or an "F" from a box containing 10 of each; the same order of presentation was used with all birds to facilitate analysis. Both total consumption and length of first feeding flight (= time hovering at feeder before returning to perch during first flight after feeder change) were measured daily. Birds were weighed daily to determine if they lost weight on the non-preferred sugar. Prior to the experiment, all birds had been weighed daily for 10 days, to accustom them to the experience.

Results: The total consumption of sucrose over the 10 days (120 hr, or 600 bird-hr) was 279 ml, or 0.464 ml/bird-hr. Consumption of fructose was virtually identical: 267 ml in 118 hr (590 bird-hr), or 0.458 ml/bird-hr. No clearcut pattern of weight changes was evident (table 2). On the average, birds lost weight only when given fructose for the second day in a row, and this is largely the result of one bird's losing 0.6 gms on one day. Aside from this, the largest daily weight change was 0.3 gms, with changes in different birds tending to cancel in most cases. There is great variability in the times of the first feeding flight (table 2), but the differences between initial flights to sucrose following fructose vs. fructose following sucrose were significant (Mann-Whitney U test, $U = 697$, $Z_u = 2.26$, $0.01 < P < 0.05$. Fructose may thus be taken less readily initially, but over the course of a day, the two sugars finally will be consumed in equal amounts.

EXPERIMENT 3

Do taste preferences persist, and can they be changed with conditioning?

Procedure: The experiment was done to determine if exposure to fructose only, or to a variety of sugars, could affect the initial strong preference of sucrose over fructose of birds just brought into the lab. A total of 14 birds, 5 flower-caught and 9 feeder-caught, was used. The birds were divided into groups of 6 and 8 (2:4 and 3:5 flower-caught to feeder-caught, respectively). Both groups were given 5 consecutive days of sucrose vs. fructose, then 24 days of "conditioning," then 5 more days of sucrose vs. fructose. Group 1 received 24 days of fructose during the conditioning period. Group 2 received 6 days each of sucrose, fructose, glucose, and an equal-parts mixture of all three sugars, presented in random order. All sugars were given in 30% solutions.

Results: In group 1 the aversion to fructose was weakened significantly but by no means abolished ($\chi^2 = 5.68$, $P < .05$). For group 2 the effect of the conditioning is not significant ($\chi^2 = 2.41$, $P > 0.5$) (table 3). The most that I can conclude from this experiment is that if the sucrose-over-fructose preference can be abolished, a much longer conditioning period will have to be used. The results attest more to the strength of taste preferences than to their lability.

TABLE 3. Amounts of sucrose and fructose consumed by 2 groups of Anna Hummingbirds before and after 24 days' conditioning to fructose only (group 1) or various sugars (group 2).

	Amt. S consumed (ml)	Amt. F consumed (ml)	Total consumed (ml)	No. bird-hours
Group 1: Given fructose only for 24 days between initial and final trials. 6 birds.				
Initial	157	42	199	366
Final	120	58	178	359
Group 2: Given 6 days each of sucrose, glucose, fructose, mixture between initial and final trials. 8 birds.				
Initial	188	59	247	477
Final	156	69	225	453

Difference between initial and final trials significant for group 1 ($\chi^2 = 5.68$, $P < .05$), not group 2 ($\chi^2 = 2.41$, $P > .05$). In all cases difference between sucrose and fructose consumed is highly significant ($P < .01$).

EXPERIMENT 4

What sugar concentrations do Anna Hummingbirds prefer, and do they prefer different concentrations of different sugars?

Procedure: These experiments involved 3 groups of 5 feeder-caught birds each for 10 days. The members of each group received a choice between 15%, 30%, and 45%, or 30%, 45%, and 60% solutions of a particular sugar—the members of a group received the same sugar throughout. The sugars used were sucrose, glucose, and fructose; which set of concentrations a bird received on a given day was determined by drawing "high" or "low" cards out of a bag containing 10 of each. Relative caloric intake was calculated by multiplying the amounts consumed of 15%, 30%, 45%, and 60% solutions by 1, 2, 3, or 4, respectively. Immediately following this experiment, the fructose birds were given 30–45–60% sucrose, and the sucrose birds were given 15–30–45% fructose, to see if exposure to one sugar affected the preference for different concentrations of the other sugar.

Results: The birds clearly preferred the highest concentrations available of sucrose and glucose, but rejected high concentrations of fructose in favor of lower ones (table 4). Relative caloric intakes were higher for the more concentrated sugars. As there was no apparent difference in activity between birds receiving higher or lower concentrations, the birds may have been more efficient at metabolizing the less concentrated solutions. When switched from a sugar preferred at high concentrations to one preferred at low concentrations, the birds briefly preferred the second sugar at higher concentration—and vice versa (table 5). Taste conditioning to high or low concentrations might therefore occur. This 'concentration conditioning' mght temporarily override sugar preferences, but the latter were reestablished within 3 days.

EXPERIMENT 5

Do species differ in taste preferences?

Procedure: I have sufficient data on sugar preferences of three other hummingbird species to compare with the results for the Anna Hummingbird. These include 2 California species, the Rufous (*Selasphorus rufus*) and Black-chinned (*Archilochus alexandri*) hummingbirds, and the tropical Fork-tailed Woodnymph (*Thalurania furcata*). The Rufous Hummingbirds were all immatures captured in fall migration, the Black-chinned Hummingbirds were adults caught on the breeding grounds early in the breeding season. The *Thalurania* were captured during a field trip to northeastern Nicaragua in April 1967. A total of 5 *Thalurania* (4 males, 1 female), 4 *Archilochus* (2 male, 2 female), and 5 *Selasphorus* (2 male, 3 female) were used. The *Thalurania* received various combinations of sucrose, fructose, and glucose at 30% or 20%, and also were given 30% vs. 20% choices for each sugar. Each bird received each combination on 3 different days. The California species received various paired combinations of 30% sucrose, glucose, fructose, and an equal-

TABLE 4. Amounts consumed of different concentrations of 3 sugars, by 5 Anna Hummingbirds for 5 days at each set of concentrations. Each bird received only 1 sugar.

	Concentrations			Total consumed (ml)	Relative caloric intake	Concentrations			Total consumed (ml)	Relative caloric intake
Sugar	15%	30%	45%			30%	45%	60%		
Sucrose	12	49	109	170	437	16	50	82	148	498
Glucose	13	53	110	176	449	26	28	100	154	536
Fructose	120	94	41	275	431	164	42	4	210	470

Differential consumption of different concentrations of each sugar is highly significant ($P < .01$) in all cases. Consumption of different concentrations of fructose differs significantly ($P < .01$) from consumption of different concentrations of sucrose and glucose.

TABLE 5. Change in preferred sugar concentrations of Anna Hummingbirds, when switched from a sugar preferred at high concentrations (sucrose) to one preferred at low concentrations (fructose) or vice versa.

Days following switch	Switched from sucrose to fructose amounts (ml) consumed:			Switched from fructose to sucrose amounts (ml) consumed:		
	15% F	30% F	45% F	30% S	45% S	60% S
1	7	13	20	22	7	6
2	11	19	9*	6	16	14**
3–6	90	50	12**	25	43	64

Asterisks denote level of significance of difference in consumption of different concentrations from consumption on previous day.

parts mixture of all three; two days per bird per 2-sugar combination.

Results: Individual woodnymphs varied considerably in their responses to different sugars, and significant heterogeneity existed in several comparisons (table 6). Leaving aside individual variation, as a group the *Thalurania* preferred sucrose over glucose over fructose at 30%, glucose over sucrose over fructose at 20%, and 30% over 20% glucose and sucrose, 20% over 30% fructose.

The same order of sugar preferences at 30% was shown by both Rufous and Black-chinned hummingbirds (table 7). The mixture was preferred over glucose by all Rufous Hummingbirds, and by two of the Black-chinned Hummingbirds. Nearly all birds of both species preferred the mixture to fructose.

Sugar preferences of all four species, including *C. anna* (table 1) were fairly similar. The preference order sucrose > glucose > fructose obtained for all groups except the *Thalurania* at 20%; there was considerable individual variation in the sucrose vs. glucose comparison. Nearly all birds rejected fructose in any combination. There was more variation, both among species and among individuals of the same species, in the response to the mixture.

EXPERIMENT 6

Do wild hummingbirds become conditioned to the colors of their preferred flowers?

Procedure: In natural chaparral habitats, the flower most visited by Anna Hummingbirds during the winter and spring is *Ribes speciosum*, which is red. Rufous Hummingbirds in spring migration are also largely dependent upon *Ribes* flowers. In late summer and fall, the yellow-flowered *Nicotiana glauca* is the most visited by both species, although some *C. anna* also feed at the red-flowered *Zauschneria cana* (Stiles 1973). In this experiment, birds captured at *Ribes* and *Nicotiana* were given a choice between red and yellow feeders as soon as they were brought in from the field. Ten Anna and three Rufous hummingbirds caught at *Ribes*, and nine Anna and seven Rufous hummingbirds caught at *Nicotiana* were used. As I was interested mainly in the initial reactions to the two colors, each bird was tested for only 4 to 5 hr. Responses of each bird were scored as "preference" or "no preference," based on whether the amounts consumed from the two feeders differed significantly from the null hypothesis of 50:50 by a χ^2 test. Because of the short duration of the experiment, position effects were ignored: hopefully, birds just introduced into the cages would not have had time to develop cage stereotypes.

Results: Ignoring those birds that showed no preference, the difference between *Ribes*-caught and *Nicotiana*-caught birds was highly significant (table 8). Both species preferred red when caught at *Ribes*, and yellow when taken at *Nicotiana*. A number of *Nicotiana*-birds did show a preference for red, however; this may indicate that much of their feeding was done at *Zauschneria*.

TABLE 6. Amounts of different sugar solutions consumed (ml) by 5 Fork-tailed Woodnymphs (*Thalurania furcata*).

30% S vs. 30% G (49–28)*	30% G vs. 30% F 61–11**	30% S vs. 30% F 56–22**
20% S vs. 20% G (56–80)*	20% G vs. 20% F (82–39)**	20% S vs. 20% F 105–25**
30% S vs. 20% S 58–27**	30% G vs. 20% G 51–37	30% F vs. 20% F 58–93**

For abbreviations and symbols see table 1.

TABLE 7. Amounts of different 30% sugar solutions consumed by Rufous and Black-chinned hummingbirds.

Sugars	S vs. G	S vs. F	F vs. G	S vs. M	G vs. M	F vs. M
Amounts consumed (ml): Rufous Hummingbirds	44–16**	33–18*	7–42**	32–16*	15–38**	(20–28)
Amounts consumed (ml): Black-chinned Hummingbirds	(21–18)	26–16	12–33**	24–15	(21–23)	13–30**

For symbols and abbreviations see table 1.

EXPERIMENT 7

What is the relative importance of taste and color preferences in *C. anna*? To what extent are color preferences modifiable by taste preferences, and how rapidly does this modification take place?

Procedure: The experiment was divided into 4 parts. In part 1, birds were given a choice between sucrose and glucose, until a consistent taste preference had been established. In part 2 the birds were offered a choice between red and yellow feeders containing SFG mixture until a consistent color preference was established (5 consecutive choices of the same sugar or color, during which interval the sugar or color had appeared at least once in each of the two positions). In part 3, birds were offered a choice between one feeder combining the preferred sugar and non-preferred color, and another combining the preferred color and non-preferred sugar, to test the relative strengths of taste and color preferences. When 3 consecutive choices of a sugar-color combination had been made, the birds moved to part 4, which was essentially a repeat of part 2, to see if the original color preferences had been modified by the experience of part 3.

Fourteen Anna Hummingbirds were caught in a *Eucalyptus* grove in October 1968, and began the experiment within 3 days of capture. All birds completed part 1, but 3 birds failed to establish consistent color preferences in part 2 and were disqualified. One bird died during part 3 and one during part 4, leaving 9 birds that completed the entire experiment.

Results: In all cases, the taste preferences of phase 1 were quickly established: only 5 to 7 trials were necessary for a bird to make the requisite 5 consecutive choices of one sugar: 13 of 14 birds preferred sucrose (fig. 2). Consistent color preferences in phase 2 were much more difficult to establish, and 3 birds failed to do so in 15 days. Six of 11 birds preferred yellow over red, perhaps reflecting the importance of white or yellow (*Eucalyptus* and *Nicotiana*) flowers at that time of year; however, gardens with red hummingbird-visited flowers were near at hand.

In part 3, 8 birds chose the preferred color over the preferred sugar on the first day, but all 10 surviving birds eventually chose the preferred sugar consistently—no bird required more than 6 trials to make the requisite 3 consecutive choices. This indicates that taste preferences will quickly override color preferences (table 9).

In part 4, six of 10 birds initially chose the originally non-preferred color, which had been associated with the preferred sugar in part 3. In the absence of differential reinforcement, four of these birds gradually switched back to the originally preferred color. Four birds chose the originally preferred color on the first day, but two of the three survivors of this group ended up showing no consistent color preferences (fig. 2, table 9).

TABLE 8. Color preferences of Anna and Rufous hummingbirds captured at *Nicotiana* (yellow flower) in the fall, or *Ribes* (red flower) in the spring.

Species of		No. birds preferring:		
Hummingbird	Flower	Red	Yellow	No preference
Anna	*Ribes*	8	1	1
	Nicotiana	3	4	2
Rufous	*Ribes*	3	0	0
	Nicotiana	2	4	1
Total[a]	*Ribes*	11	1	1
	Nicotiana	5	8	3

[a] $\chi^2 = 5.45$, $P < .025$, excluding those birds that showed no preference.

TASTE AND COLOR STIMULI PRESENTED BY HUMMINGBIRD FLOWERS

This section presents the results of my field observations of flower visitation by hummingbirds in California and Costa Rica. My objective was to determine which flowers were preferred by hummingbirds, and to examine the taste and color stimuli presented by these

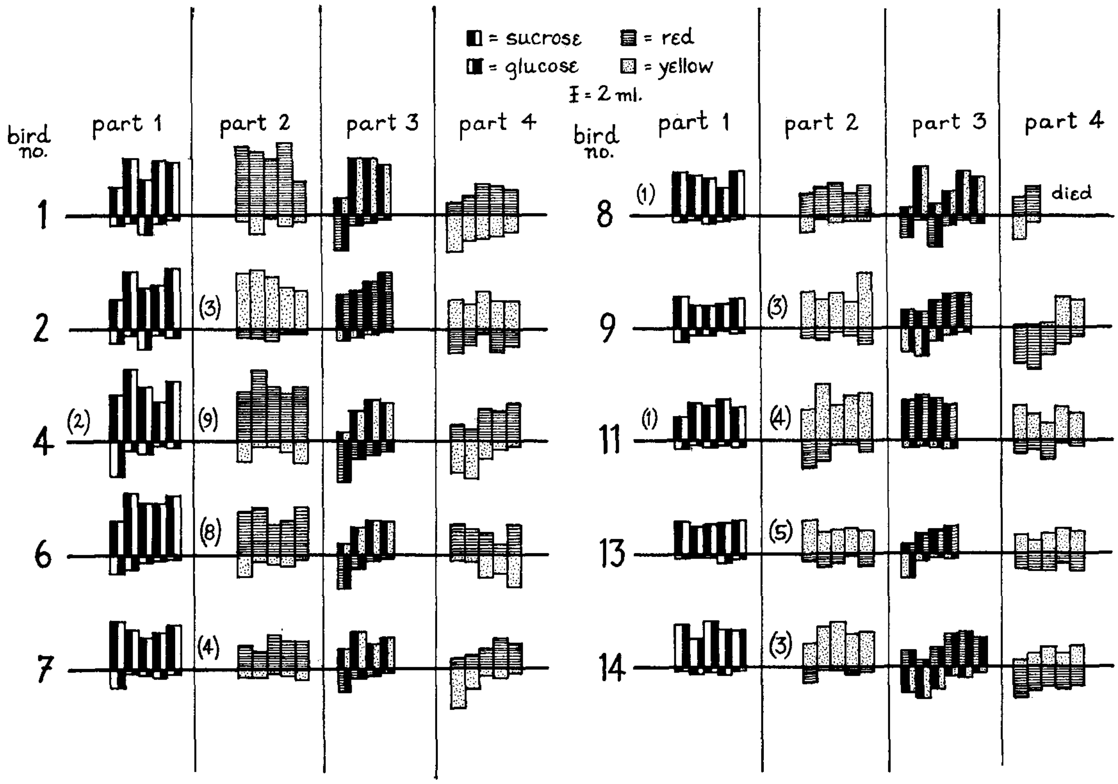

FIGURE 2. Relative strengths of taste and color preferences in Anna Hummingbirds, as demonstrated by Experiment 7 (see text). The final 5 trials of parts 1 and 2, and all trials of parts 3 and 4 are shown. Numbers in parentheses for parts 1 and 2 are the number of trials (if any) preceding the final 5 trials. Ml consumed of the favored sugar, color, or combination thereof, are plotted above the horizontal line; consumption of the non-preferred solution is plotted below the line.

flowers. These stimuli were further considered in relation to possible specializations for hummingbird pollination. In this paper, I consider a flower to be specialized for pollination by hummingbirds if it is morphologically adapted for pollination by any species of hummingbird in the community, regardless of whether it is pollinated or even visited by other species. Similarly, I consider a flower to be preferred by hummingbirds irrespective of the number of species that do prefer it.

TABLE 9. Effect of changing sugar solutions on color preferences in Experiment 7 (see text).

	Consumption[a] of solution displaying:		
Trial	Originally preferred color	Originally non-preferred color	Interpretation
A: Final, pt. 2	49.5	12.7**	Color preference established
B: Initial, pt. 3	(36.7	25.8)	Variability in response: preferred sugar combined with nonpreferred color
C: Final, pt. 3	6.1	50.1**	Preferred sugar chosen over preferred color
D: Initial, pt. 4	(23.9	31.2)	Variability in response to colors without differential reinforcement
E: Final, pt. 4	(31.6	17.1)*	Original color preference reestablished in many cases

[a] Summed consumption of all birds, in ml. For other abbreviations and symbols see table 1.
Significance levels of chi-square tests comparing results of different trials: A/C**, A/E n.s., C/E**.

METHODS AND MATERIALS

The hummingbird-flower community that I studied most intensively was in the Santa Monica Mountains, Los Angeles County, California. Between January 1967 and June 1970, I observed hummingbird foraging in natural chaparral and oak woodland as well as in gardens and plantings of various types. The specific study areas were described by Stiles (1973).

In Costa Rica, I made extensive observations of the hummingbird-flower community of Finca La Selva, in the wet Caribbean lowlands. The major habitats here were tropical wet or "rain" forests and various stages of second growth (cf. Slud 1960, Stiles 1975). These studies were made chiefly between February 1971 and March 1974. Between 1969 and 1974 I also made numerous visits to a highland hummingbird-flower community on Cerro de la Muerte at about 3000 m elevation. The area and its hummingbirds have been described by Wolf (1969) and Wolf and Stiles (1970).

Instances of hummingbirds foraging at flowers were recorded during census walks, by spending time observing at different potential food plants, or in the course of observations on hummingbird territoriality, nesting, etc. Due to patchy distribution of flowers in space and time, including changing abundances and dispersion of alternative food flowers, a fully quantitative and objective assessment of hummingbird foraging preferences is beyond the scope of this paper. Rather I have devised a qualitative rating system for hummingbird food flowers based upon foraging patterns that I saw. Although largely subjective, this system makes clear the kinds of evidence upon which a flower's rating is based. The ratings are:

1. Highly preferred.
   a. When common, visited more frequently than other flowers of comparable abundance.
   b. When rare, sought out and visited out of proportion to abundance.
   c. When common and defendable, consistently supports territorial hummingbirds.
2. Weakly preferred.
   a. Visited frequently when common, seldom when rare; about in proportion to its abundance.
   b. Supports territorial birds only when very abundant, even then not consistently.
3. Not preferred.
   a. Rarely visited, regardless of abundance.
   b. Never supports territorial birds.

The pollination system of flowers is also very important from an evolutionary and theoretical point of view. For as many flower species as possible, I tried to assess the efficacy of hummingbirds as pollinators. While it may be relatively easy to observe a bird carrying a pollen load, it is often difficult to determine if the pollen consistently contacts stigmas of the appropriate flower and is deposited on them. Extensive bagging experiments to evaluate fruit set would be required in many cases to prove hummingbird pollination, and these were beyond the scope of my study. I divided hummingbird-visited flowers into five categories according to my evidence (or lack thereof) for hummingbird pollination:

A. Pollen load picked up and carried by bird, and observed to contact stigmas of appropriate flowers consistently ($\geqslant 50\%$ of at least 10 visits).

B. Frequently visited by hummingbirds; morphology suggests hummingbird pollination (cf. Grant and Grant 1968) but pollen transfer (including deposition on stigmas) not confirmed; hummingbird pollination likely but not proven.

C. Some pollen picked up and carried by bird, but stigmas of appropriate flowers not contacted consistently ($< 50\%$ of at least 10 visits).

D. Frequently visited, but probably not pollinated, by hummingbirds; morphology not suggestive of hummingbird pollination; pollen transfer not seen.

E. Infrequently visited by hummingbirds; pollen transfer not observed; hummingbird pollination highly unlikely on morphological grounds as well.

Further observations on some of these flowers might change their classification in the above system.

Flower nectar was collected with fine capillary tubes (10, 25, or 100 microliter tubes were used depending on the nectar flow of the flower). Flowers were bagged to prevent removal of the nectar by birds or insects. At intervals through the day or at the end of the day, nectar was collected to determine the amount and rate of nectar production. Some flowers could be sampled repeatedly to obtain production data directly; others, because of curves or constrictions in the corolla, had to be picked and dissected to extract the nectar, necessitating the use of different flowers for each sample. The flowers of many of these plants were found to last for several days, often with male and female parts maturing at different times. In *Ribes speciosum*, the stigma matures when the flower is about 5 to 7 days old; the anthers dehisce at age 8 to 10 days. Most other species are protandrous (e.g. *Penstemon* spp., *Diplacus*, etc.). The daily nectar flow data given are for the age stage of maximum nectar production—usually about the time the anthers dehisce.

The nectars were spotted on chromatography paper and analyzed for sugar composition by the chromatography technique of Percival (1961). After chromatographic separation of the sugars, the paper was sprayed with anisodine hydrochloride to produce different-colored spots for sucrose, glucose, and fructose. The size and intensity of these spots could be compared with the spots produced by a standard solution of equal concentrations of sucrose, glucose, and fructose run concurrently to determine semiquantitatively the relative amounts of these three sugars.

Sugar concentrations of nectars of many Costa Rican flowers were measured with a temperature-compensated hand refractometer (cf. Wolf et al. 1972) while those of a few California species were measured by freezing point depression. The latter data were difficult to interpret and were not entirely comparable to the refractometer data. Hence, nectar concentration will not be discussed in any detail in this paper.

Colors of hummingbird-visited flowers proved more difficult to characterize objectively. I described the colors(s) of each flower as precisely as possible, and measured spectral reflectances of the corollas of several species. These measurements were made over the 400 to 700 millimicron wavelength range of the spectrum using a Beckman G2 spectrophotometer equipped with a reflectance unit (cf. Norris 1967).

RESULTS

Lists of the color, daily nectar flow, preference rating, and pollination class of hummingbird food plants in the Santa Monica Mountains, California and the Costa Rican sites can be obtained from the author. For each of

TABLE 10. Colors and preference ratings of California flowers.

Preference rating	Crimson Magenta Pink	Red Scarlet	Vermilion Orange	Any of these in combination	Yellow	Green	Blue Lavender	Violet Maroon	White Cream	Total
A. Native flowers										
1	1	4	2	1	0	0	1	0	0	9
2	2	0	0	0	0	0	3	1	2	8
3	0	0	0	0	3	0	1	1	3	8
B. Exotic flowers[a]										
1	2	8	2	2	1	0	0	1	3	19
2	1	6	1	3	1	0	0	1	3	16
3	1	2	0	0	0	0	1	1	2	7
C. All flowers[a]										
1	3	12	4	3	1	0	1	1	3	28
2	3	6	1	3	0	0	3	2	5	24
3	1	2	0	0	3	0	2	2	5	15

[a] Different color varieties of some species are tabulated separately.

these flower species, I observed at least one instance of hummingbird visitation. Some flowers are visited rarely (and then only by inexperienced young birds), while others form the staple food supply of some hummingbirds at certain seasons (Stiles 1973). It is important to note that a hummingbird's staple food flower need not be very highly preferred, if no choice is available. For instance, in late fall when no other flowers are available *C. anna* depend on the flowers of *Ribes malvaceum* and *Arctostaphylos glauca*, but they largely desert these as soon as *Ribes speciosum* becomes available (Stiles 1973). *C. costae* is highly dependent upon *Salvia* flowers in many areas, but prefers *Penstemon cordifolius* when it is available.

Among native California chaparral flowers, all highly preferred species (= those with a preference rating of 1 in at least some situations) have colors in the long-wavelength end of the visible spectrum: some shade of red or orange, or colors like magenta with a strong long-wavelength component (table 10). Weakly preferred or nonpreferred flowers are pink, white, yellow, or short-wavelength colors. Among native flowers, a preference rating of 1 is also strongly correlated with a high nectar flow. No chaparral flower with a daily nectar flow of less than ca. 15 μl/day is highly preferred, and no weakly or nonpreferred flower has a nectar flow of much over 10 μl/flower/day. Moreover, the same 9 species are highly preferred in each case: long-wavelength colors and high nectar flow go together (see below). However, this makes it difficult to distinguish between color and nectar flow as factors in flower choice of chaparral hummingbirds.

Large gardens often offer hummingbirds a much greater choice of flowers within a small area than is usually the case in the wild, both in terms of colors and range of nectar flow. Most of the highly-preferred exotic flowers have long-wavelength colors, but this is by no means always the case. Some red or orange flowers are weakly preferred or not preferred, while several white or yellow flowers have a preference rating of 1 (table 10). Thus, color does not appear to be as good a predicter of hummingbird flower preferences in gardens as in the wild. On the other hand, the correlation of high preference ratings with high nectar flow still holds among the exotic flowers, although the situation is more complicated (table 11). No flower with a preference rating of 1 has a nectar flow of under ca. 15 μl/day, and most have daily nectar production of 25 μl or more. However, some flowers with moderate to high nectar flows are only

TABLE 11. Nectar flow in relation to preference rating in native and exotic California flowers.

Preference rating	Nectar flow (μl/flower/day)				
	< 10	10–24	25–50	50+	Total
A. Native chaparral flowers					
1	0	6	3	0	9
2	4	4	0	0	8
3	7	1	0	0	8
B. Exotic flowers					
1	0	1	4	6	11
2	2	1	1	2	6
3	5	2	0	0	7
C. All flowers					
1	0	7	7	6	20
2	6	5	1	2	14
3	12	3	0	0	15

TABLE 12. Nectar flow in relation to pollination category in native and exotic California flowers.

Pollination category	Nectar flow (µl nectar/flower/day)				
	< 10	10–24	25–50	50	Σ
A. Native chaparral flowers					
AB	0	6	3	0	9
B*C	4	1	0	0	5
DE	8	3	0	0	11
B. Exotic flowers					
AB	0	2	3	1	6
B*C	0	0	2	7	9
DE	5	3	0	0	8

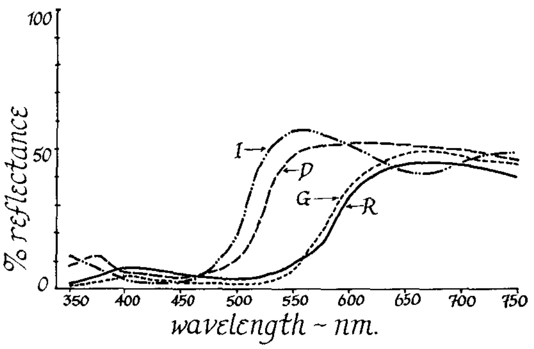

FIGURE 3. Spectral reflectance curves of corollas of several California flowers visited by hummingbirds. I = *Isomeris arborea* (yellow); D = *Diplacus longiflorus* (orange); G = *Galvezia speciosa* (red); R = *Ribes speciosum* (red).

weakly preferred or even nonpreferred, and clearly other factors are playing a major role in these cases. For example, in *Erythrina* spp. nectar is abundant but the corolla tube is relatively long, making the nectar available to the hummingbird considerably less than the total nectar flow. Nectar composition may also be important in some instances (see below). Even taking these complications into account, it is evident that nectar flow better predicts hummingbird preferences than does color in this situation.

A flower's pollination class to some degree relates the amount of hummingbird visitation to the degree of morphological specialization for hummingbird pollination. In general, the native California flowers with high preference ratings can be characterized morphologically by a tubular corolla, colors in the long-wavelength end of the visual spectrum and in particular, high nectar production. This is in essence the "hummingbird pollination syndrome" (cf. Faegri and van der Pijl 1966, Grant and Grant 1968), and these characteristics are shown by all hummingbird-pollinated chaparral flowers (tables 10 and 13). In fact, I found no native flower apparently adapted for hummingbird pollination that was not also highly preferred, in at least some situations. Conversely, all highly preferred chaparral flowers were also hummingbird-pollinated. This doubtless reflects the key role played by high nectar production in specializing for hummingbird pollination.

Pollination classes C and D contain flowers frequently visited by hummingbirds but probably not pollinated by them. The most prominent examples among native California flowers are several species of *Salvia*. These flowers are regularly visited only by *Calypte costae*, apparently reflecting the habitat choice and subordinate status of this species. *Ribes malvaceum* and *Arctostaphylos glauca* show a lesser degree of (perhaps incipient) specialization for hummingbird pollination, "bill-tip pollination," (cf. Grant and Grant 1968, see also Stiles 1973).

Among the cultivated and naturalized flowers in tables 10–12 are several that combine high nectar flow and high preference ratings with obvious lack of specialization for hummingbirds. Most of these flowers are adapted for pollination by birds other than hummingbirds, and are designated by B* in the tables. Examples include several sunbird-pollinated species from Africa (*Aloe* spp., *Strelitzia*, *Erythrina* spp., etc.) and honeyeater (Meliphagidae)-pollinated Australian species (*Callistemon*, *Eucalyptus* spp.), as discussed by Skead (1967), Officer (1964), and others. Other exotic flowers favored by California hummingbirds are neotropical species specialized for hummingbird pollination: *Cestrum*, *Jacobinia*, *Nicotiana*, *Heliconia*, etc. The nectar flow of these species, while high relative to that of insect-pollinated species, is often lower than that of ornithophilous flowers from Africa and Australia, which are adapted for pollination by larger birds.

Further insight into the role of color in the "hummingbird pollination syndrome" can be gained by comparing the spectral reflectance curves, over the 400 to 700 nm wavelength range, of several important hummingbird food plants of California (figure 3). These include two red flowers (*Ribes*, *Galvezia*), one orange (*Diplacus*), and one yellow (*Isomeris*). *Ribes* and *Diplacus* are important food sources for hummingbirds in the coastal chaparral, *Isomeris* in the Mojave Desert, and *Galvezia* on the Channel Islands (Stiles 1973 and unpubl. data). These reflectance curves are strikingly similar in their general shape. All have a broad peak of reflectance in

TABLE 13. Colors of Hummingbird pollinated flowers (including inflorescences) of different areas.

Area	Colors											
	Crimson Magenta Pink	Red Scarlet	Ver-milion Orange	Any of these in com-bination	Yellow	Green	Blue Laven-dar	Violet Maroon	White Cream	Total	% Solid Red	% with conspicuous long-wavelength colors in "flag"
California												
Chaparral	1	4	2	1	0	0	1	0	0	9	66.7	88.9
Exotic	1	2	1	3	1	0	0	0	0	8	50.0	87.5
Cerro de la Muerle	2	4	2	4	2	0	0	0	0	14	57.2	85.7
La Selva	3	9	6	15	4	0	0	0	1	37	50.0	85.6
Totals	8	19	11	23	7	0	0	0	1	68	—	—

the long-wavelength end of the spectrum, falling off rapidly to low reflectances at shorter wavelengths. The curves differ mainly in the location of the drop from high to low reflectance going towards the shorter wavelengths, and all of the wavelengths of 50% (of maximum) reflectance fall within a range of 100 nm. Corollas of *Diplacus* and *Isomeris* are similar in their reflectances; the former is probably hummingbird-pollinated, the latter probably is not (cf. Grant and Grant 1968).

Distributions of colors of hummingbird-pollinated flowers are similar in the various communities studied (table 13). Nearly all species have some long-wavelength color (anything between magenta and vermilion) prominently displayed as a "flag" to attract hummingbirds. The communities differ chiefly in the relatively large number of species at La Selva having a long-wavelength color in combination with another color in the flag (red and yellow, red and green, red and white, etc.). This is mainly because many hummingbird-pollinated plants at La Selva bear their flowers in large, long-lived inflorescences (e.g. *Heliconia*, bromeliads). The inflorescence itself is often red or red and yellow and probably serves as the flag for attracting hummingbirds; the flowers themselves are of a color that contrasts with the inflorescence—often green, yellow, or pink)—enabling the bird, once at the inflorescence, to find them quickly. The flowers are short-lived, so that the main temporal continuity in flower-seeking visits by the birds is maintained by the colorful inflorescence (cf. Stiles 1974).

TABLE 14. Nectar composition and preference ratings of native and exotic California flowers.

	Preference rating	High su-crose	Bal-anced	Low su-crose	Totals
Calif. native flowers	1	7	1	0	
	2	0	5	0	
	3	0	2	2	
Exotic flowers	1	5	2	3	
	2	0	1	1	
	3	0	0	1	
All flowers[a]	1	12	6		18
	2 + 3	0	12		12

[a] $\chi^2 = 10.70$. $P < .005$.

Data on sugar composition of the nectars of various hummingbird food flowers may be obtained from the author. The composition of nectars is relatively constant within a species, but the concentration may vary considerably (see also Percival 1961). For statistical analysis, I recognized 3 types of nectar:high-sucrose (sucrose minus glucose/fructose concentrations $\geqslant +1$ in the semiquantitative system given above); balanced (sucrose minus glucose/fructose concentrations between +1 and −1 inclusive); and low-sucrose (sucrose minus glucose/fructose concentrations less than −1).

Among native California flowers, highly-preferred flowers tend to have high-sucrose nectars, while weakly or nonpreferred flowers have balanced or low-sucrose nectars (table 14). Among the exotic flowers grown in California, the picture is more complicated. Nectar-rich, highly preferred flowers may not have high-sucrose nectars, but seldom have nectars high in fructose. One flower having a copious, relatively high-fructose nectar is *Melianthus* (*Thunbergia*) *major*, which is rarely visited by hummingbirds. The association of high-sucrose nectars and a preference rating of 1 is highly significant (table 14).

The tendency for hummingbird-pollinated species to have nectars high in sucrose (table 15) is particularly striking within genera like *Ribes*, *Salvia*, and *Penstemon*; the hummingbird-pollinated members of these genera

TABLE 15. Nectar composition and pollination category of hummingbird flowers of California and Costa Rica.

	Nectar composition		
Pollination category	High-sucrose (S-GF> +1)	Balanced (+1⩾ S-GF⩾−1)	Low-sucrose (S-GF<−1)
AB	23	3	0
B*	1	2	4
C	0	5	0
DE	0	2	3
Total non-hummingbird pollinated	1	9	7

	High sucrose	Balanced or low sucrose	
Hummingbird pollinated	23	3	$P < 0.001$
not hummingbird pollinated	1	16	$\chi^2 = 19.34$

have high-sucrose nectars, the insect-pollinated members have balanced nectars. High-sucrose nectars are found in hummingbird-pollinated flowers of all areas studied: native California and Costa Rican species, and exotics from Central and South America growing in California gardens. On the other hand, ornithophilous flowers from the Old World have nectars that are balanced or low-sucrose rather than high-sucrose (table 15).

DISCUSSION

COMPARISON OF LABORATORY AND FIELD DATA

In general, the laboratory experiments suggest the following hierarchy of factors in feeder choice: energetic factors over taste (sugar composition) over color. A nonpreferred sugar, fructose, was taken in equal amounts as the preferred sugar sucrose if no choice was offered. Taste preferences can apparently determine color choice if energetic factors are equalized (experiment 7). These data agree with the results of Collias and Collias (1968), who found that sucrose concentration was more important than color or position in determining feeder choice. My experiments indicate that Anna Hummingbirds prefer sucrose and glucose in the highest concentrations available, up to 60%, even though they may be less efficient at metabolizing these solutions (see above). This apparently lower efficiency may reflect the rarity of such concentrated solutions in nature; most flower nectars are around 30% or less (tables 14 and 15; Hainsworth and Wolf 1972, Stiles 1975). The preference for high concentrations of sucrose or glucose of the Anna Hummingbird accords with Van Riper's (1960) results for the Broad-tailed Hummingbird (*Selasphorus platycercus*). However, Ruschi (1953) found that several Brazilian species preferred sucrose concentrations of 15–25% over stronger or weaker solutions. My results (table 5) indicate that Ruschi's birds may have been conditioned to the concentrations of nectars in their local food flowers, as Ruschi himself suggested. Why such conditioning apparently does not occur in North American species remains to be seen.

At feeders, with unlimited "nectar," the main factor affecting energetics is sugar concentration. The major energetic parameters of flowers are the amount and concentration of nectar, along with the efficiency of nectar extraction by the birds (Wolf et al. 1972). In the wild, one would thus expect hummingbirds to prefer flowers producing either the greatest quantity of nectar, or the most concentrated nectar. Good data on nectar concentrations are lacking for most flowers, but the available information suggests that nectar concentrations vary over a relatively small range compared to total nectar production, at least within the flowers of a single community (table 10; see also Hainsworth and Wolf 1972, Stiles 1975). Among both native and exotic flowers in California, the flowers having the highest nectar flow are the ones most preferred by hummingbirds.

The importance of energetic factors in determining response to different colors is shown by Experiment 6, in which the color of the most rewarding food flower changed seasonally, and responses to color of the hummingbirds changed likewise, as was also found by Wagner (1946) for several Mexican species. The preference for nectar-rich flowers in the wild is probably analogous to the preference for concentrated sugar solutions in the laboratory, in that both would tend to maximize energy intake by the bird.

All four species of hummingbirds tested here preferred sucrose over glucose over fructose, with an equal-parts mixture of all three sugars falling somewhere in the middle. The same order of preference was found in the Broad-tailed Hummingbird (Van Riper 1960) and apparently occurs in several other tropical species (Stiles, unpubl. data). In the field, in both tropical and temperate-zone areas flowers specialized for hummingbird pollination have nectars high in sucrose. This strongly suggests that a preference for sucrose is widespread among hummingbirds, and that a part of the complex of adaptations for hummingbird pollination may be the production not only of copious nectar, but of sucrose-rich nectar as well. Ornithophilous flowers from other continents may not have nectar particularly high in sucrose. The sucrose preference of hummingbirds may not be shared by sunbirds, honeyeaters, flowerpeckers, or other Old World nectarivores.

One could argue that the sucrose preference of hummingbirds in the laboratory is an artifact of their preference for flowers of high nectar flow—which also happen to have high-sucrose nectars. However, this does not explain the correlation of nectars rich in sucrose with other characteristics indicative of specialization for hummingbird pollinators, within several plant genera. The exotic flowers listed in tables 11 and 14 demonstrate no necessary functional correlation between producing large quantities of nectar and producing high-sucrose nectar. The sucrose preference of hummingbirds caught in gardens, where many highly preferred flowers have nectars not particularly rich in sucrose, also suggests more than sucrose conditioning.

Experiments 2 and 7 indicate that taste preferences are less labile than are color preferences. Taste preferences can determine color choice if energetic factors are equal even if both sugars (e.g. sucrose and glucose) are relatively highly preferred, suggesting that, under some circumstances, nectar composition might be an important factor in flower choice. To some extent at least, this does occur in the field since certain moderately nectar-rich flowers with low-sucrose nectars (*Melianthus* and perhaps *Scrophularia*) are not preferred by hummingbirds.

The role of position factors was not treated in this paper. However, several parameters associated with the spatial distribution of food frequently may be confounded. Hummingbirds have on several occasions been shown to learn and remember the location of a single feeder in a large area with great accuracy over a period of several months (Bené 1945, Miller and Miller 1971). This level of spatial memory is doubtless analogous to remembering the location of a bush or clump of flowers from one blooming season to the next, an obvious asset to a long-lived bird in a habitat where blooming seasons are short. On the other hand, hummingbirds' memory for the location of a particular feeder within a closely-packed array is less good, especially in the absence of visual cues (Miller and Miller 1971). The advantage of this "within flower clump" level of spatial memory to a bird probably lies in enabling it to recall which flowers it visited most recently (and thus depleted of nectar), and to visit other flowers on its next foraging flight. There is evidence that some species have this capacity (Stiles, unpubl. data, Ortiz-Crespo 1967). With feeders, the consequence of one foraging bout would not affect the location of available nectar for the next bout; remembering the feeder last visited and avoiding it on succeeding foraging flights could easily lead to choice of the wrong feeder. Therefore, the results of any position experiments using feeders must be interpreted with great caution. Position factors may also be important energetically, especially in the wild, because they can affect the cost of exploiting flowers of different dispersion patterns. It is thus not surprising that position can override color in feeder choice of some hummingbirds (Collias and Collias 1968).

Color is hence an orienting stimulus, perceived at a distance, that directs birds to the reward—flower nectar or sugar-water. The value and prevalence of particular colors as orienting stimuli probably depend heavily on the properties of avian eyes and perhaps the visual systems of other potential flower visitors. The food reward of a flower or feeder must be perceived by the sense of taste. It is this reinforcement for the association of color with food that has long been mislabeled "color preference."

AVIAN SENSES AND POLLINATION BY HUMMINGBIRDS

The few avian species whose color vision has been studied show peaks of spectral sensitivity and hue discrimination about 20 nm towards the longer wavelengths, compared with man (Honigmann 1921, Blough 1957, Adler and Dalland 1959, Ikeda 1965). This is generally ascribed to the filtering action of the retinal oil droplets (Donner 1960). The oil droplet absorption spectrum of the Anna Hummingbird closely resembles that of the relatively well-studied pigeon, *Columba livia* (Stiles and A. Sillman, unpubl. data). Hummingbirds, like pigeons, probably can discriminate hues as well or better than man in the long-wavelength end of the spectrum. Thus, the statement that "hummingbird flowers are red" is to some extent an artifact of the human visual system. Given the similarity in spectral properties of some red, orange, and yellow hummingbird flowers, the statement loses much of its meaning. The important point is that colors of nearly all hummingbird flowers lie in the long-wavelength end of the spectrum. The frequency of red and orange as display colors of plumage (gorgets, etc.). also attests to the importance of this end of the visual spectrum to hummingbirds.

The primary requisite for the color of a hummingbird flower is that it be conspicuous to the birds, to advertise the nectar. Conspicuousness probably depends in part on the background against which the flower is displayed. Red is especially conspicuous against a background of sunlit green foliage (assuming that hummingbirds see complementary colors as man does; the frequency of yellow hummingbird flowers in plants with bluish foliage, such as *Nicotiana glauca*, suggests that they do). In shady habitats, such as the interior of tropical forest, white, yellow, and orange, perhaps in combinations with red, should be more conspicuous. In very open, sunlit habitats with little green vegetation, bright reds or yellows might be the best advertising colors.

Another factor selecting for long-wavelength colors in hummingbird-pollinated flowers may be the necessity for reducing the frequency of non-pollinating visitors, particularly insects (see Raven 1972). At least one species of bee is relatively insensitive to the red end of the spectrum (von Frisch 1950) and the spectral reflectances of most bee-pollinated flowers lie more toward the shorter visible wavelengths, or in the ultraviolet (Percival 1965). Many butterfly-pollinated flowers are red (Faegri and van der Pijl 1966), indicating that butterflies are sensitive to longer wavelengths. However, most butterflies are usually excluded from hummingbird flowers by morphological factors, and probably consume rather little nectar in any case. In tropical areas a number of short, probably insect-pollinated flowers are often visited by very small hummingbirds.

Grant (1966) proposed that the proportion of hummingbird-pollinated flowers that are red should be higher in areas inhabited by migratory hummingbirds (e.g. North America) than in areas where most species are resident ("the tropics"). The common red coloration would be learned by the birds so that they could locate flowers more quickly in their brief stays in any given area. However, the proportions of hummingbird-pollinated plants that display at least some red as an advertising color is similar (85–90%) in those temperate and tropical areas I have studied (table 3). Migration by western North American hummingbirds is not so rapid that the birds cannot investigate a variety of flowers in any locality. During spring migration, marked birds may occupy an area for up to a week, and fall migration through the mountains is still more gradual (Stiles 1973 and included references). Many of the flowers used by migrating hummingbirds are not red in any case; sapsucker drillings may be important to some species (Bent 1940, Stiles 1973). One area of the U.S. with resident hummingbirds, the Channel Islands, has red hummingbird-pollinated flowers (Grant and Grant 1968). Thus, the colors of hummingbird-pollinated flowers do not necessarily correlate with the migratory habits of the birds. Differences in color schemes among different areas are better explained in terms of differences in the lighting conditions of the habitats, or whether the flowers are conspicuous in themselves or are displayed against conspicuous, long-lived inflorescences.

The literature on the sense of taste in birds contains little that might help to explain the sugar preferences of hummingbirds. The granivorous, domesticated species studied so far show no consistency in their responses to different sugars (Kare and Medway 1959, Duncan 1960), which is not surprising since these birds normally never experience such taste stimuli. However, the results of Cameron (1947) on human subjects may be pertinent. He found the relative sweetness of fructose, sucrose, and glucose to be 173,100 (the standard), and 74 respectively. Although sweetest, fructose produced a bitter aftertaste, especially at higher concentrations. If hummingbirds taste sugars as we do, this could help to explain their rejection of fructose and preference for sucrose over glucose.

The sense of smell may also function in foraging and flower choice by hummingbirds, for recent studies have suggested that many avian species are capable of responding to olfactory stimuli (review in Bang and Cobb 1968). However, the only reasonably well-controlled experiment on the use of scent cues by foraging hummingbirds gave negative results (van Riper 1960). Most hummingbird-pollinated flowers are odorless, at least to the human nose (Faegri and van der Pijl 1966), and odor may often be a negative stimulus since most odoriferous flowers are insect-pollinated and contain little nectar. It is also possible that specific odor cues may be used at certain times, but that artificial scents such as those used by van Riper evoke no response. The strong odor emitted by flowers and foliage of *Ribes malvaceum* might help Anna

Hummingbirds to locate these plants as they come into bloom in late fall (Stiles 1973). Many tropical bat-pollinated flowers have strong odors and are frequently visited by hummingbirds at dawn or dusk (e.g. Baker 1961). The use of olfaction by hummingbirds requires further study, employing odors present in the birds' natural foodplants.

OTHER FACTORS AFFECTING FLOWER CHOICE IN THE FIELD

My field observations generally confirmed the hierarchy of factors in flower choice suggested by the laboratory experiments: energetic factors over taste stimuli over color stimuli. However, considerable variation is often evident in the preference ratings of any given flower. The major sources of this variation are differences in bill dimensions, body size, relative dominance, and habitat preference among the hummingbird species of a community. The relative importance of these factors may vary in different communities.

In my California study area, morphological variation among the 3 breeding residents is slight; even including prebreeding and postbreeding transients, the range of bill and body sizes is not greatly increased (Stiles 1973). In both Costa Rican areas, the range of bill lengths and body weights of the hummingbirds present is much greater, even though the Cerro supports only 4 species (Wolf 1969) and La Selva 20 species (Stiles, unpubl. data). Bill curvature is also important in flower choice at La Selva (Stiles 1975). Thus, morphological factors may influence flower choice much more in tropical hummingbird communities. The most important effect of differences in bill morphology may be in varying the energetic efficiency with which different species can extract nectar from different flowers (cf. Wolf et al. 1972). Also, small hummingbirds have relatively lower hovering costs, and are therefore better able to forage at flowers with relatively little nectar (Hainsworth and Wolf 1972b).

The hummingbirds of several communities are organized into interspecific dominance hierarchies (Stiles 1973, Stiles and Wolf 1970, Wolf 1969, Wolf and Hainsworth 1971). A species' position in such a hierarchy reflects its ability to compete with other species for access to nectar-rich flowers. Birds low in the hierarchy may be forced to use flowers of relatively low nectar flow. Such flowers as *Lantana* and *Lonicera* in California, *Solanum* and *Psychotria* at La Selva, and *Rubus* and *Oenothera* on the Cerro are used regularly only by the most subordinate hummingbirds in the system. Dominance position is in large part dependent on body size, with the smallest species generally being the most subordinate and, as mentioned above, best able to exploit low-nectar, often insect-pollinated flowers in any case.

Local variations in topography and moisture have produced major habitat differentiation in the dry Santa Monica Mountains of California (Stiles 1973 and included references), and this may have a major effect on flower choice. *Calypte costae* is the smallest, most subordinate breeding hummingbird in the chaparral and the only species to visit regularly the low-nectar *Salvia leucophylla*, *apiana*, and *mellifera*. These are often the only flowers present in the very dry, open slopes inhabited by this species. Both Costa Rica study areas are wet, and local habitat differences are relatively slight and dependent as much on human disturbance as upon any environmental differences (cf. Wolf 1969, Stiles 1975).

Individual differences within a species can play a complicating role in flower choice. These differences may reflect age as young, inexperienced hummingbirds in the California chaparral may try to forage at such unrewarding flowers as *Lotus* and *Encelia*, which are ignored by adults. Sex may play a role, as female hummingbirds are generally subordinate to males and may use flowers with less nectar if males are present. I cannot explain certain individual preferences, such as that of one color-marked male Anna Hummingbird in California that fed regularly at *Scrophularia*, the only hummingbird of any species to do so during my entire study.

Availability of alternate food sources also can influence preference ratings. In early winter, male *Calypte anna* seek out and defend clumps of *Ribes malvaceum* and *Arctostaphylos* when no other flowers are blooming. They may largely desert these flowers later, as the nectar-rich *Ribes speciosum* comes into bloom (Stiles 1973). On the Cerro de la Muerte in Costa Rica, *Panterpe insignis* ignores the flowers of *Centropogon valerii* when more nectar-rich flowers are available, but may be territorial at *C. valerii* when they are not (Wolf 1969).

This catalogue of complicating factors in flower choice need not undermine the validity of the conclusions of the preceding sections at the community level. One can speak of adaptations to hummingbird pollination in a general sense, independent of which species of hummingbird does the pollinating. At the species level, a number of factors operate on flower choice that may be difficult or impossible to test in the laboratory. It would, for instance, be impossible to predict from laboratory data a particular hummingbird's response to the taste and color stimuli of a flower without knowing something about potential competitors and the dominance hierarchy, availability of alternative food sources, and abundance and dispersion of birds and flowers in the available habitats.

SUMMARY

Laboratory experiments on sugar preferences and field observations on flower choice in hummingbirds indicate the following hierarchy of factors influencing preferences: energetic parameters (nectar flow of flower, concentration of feeder solution) over taste parameters (sugar composition) over color (of flower or feeder). Position factors were excluded from the experiments wherever possible because results from feeders cannot always be safely generalized to the situation in nature.

Several species of hummingbirds showed the following hierarchy of sugar preferences: sucrose over glucose over fructose, with equal-parts mixture of the three sugars falling somewhere in the middle of the preference order. The most certain result for all birds tested was the rejection of fructose, which at least in human subjects leaves a bitter aftertaste. Virtually all hummingbird-pollinated flowers studied have nectars high in sucrose. Flowers pollinated by insects, or by birds other than hummingbirds, have balanced or low-sucrose nectars. This correlation holds even among congeneric plant species having different pollinators. Thus, the production not only of abundant nectar but of high-sucrose nectar appears to be an important component in adaptation for hummingbird pollination. Some exotic flowers with low-sucrose nectars were highly preferred (but not pollinated) by hummingbirds, apparently because of their high nectar flows.

Taste preferences for glucose or sucrose solutions were effective in overriding color preferences, or in establishing new color preferences. Seasonal changes in color preferences corresponding to the color of the birds' most important food flowers suggests that color conditioning may operate in the field.

Colors of hummingbird-pollinated flowers nearly always lie in the long-wavelength end of the visible spectrum. The particular color scheme shown by a plant species probably depends mainly on the visual properties of its habitat and whether the flowers are presented individually or borne in a long-lived, colorful inflorescence. The colors of tropical and temperate-zone hummingbird-pollinated flowers are similar and do not appear to be affected by the degree of migratory behavior shown by their respective hummingbirds. Spectral properties of red, orange, and yellow flowers may be fairly similar, and hummingbirds may discriminate hues better than humans at the longer wavelengths. In the context of these factors, the question "why are hummingbird flowers red?" loses much of its meaning.

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LITERATURE CITED

Adler, H. E., and J. I. Dalland. 1959. Spectral thresholds in the Starling (*Sturnus vulgaris*). J. Comp. Physiol. Psych. 52:438–447.

Baker, H. G. 1961. The adaptation of flowering plants to nocturnal and crepuscular pollinators. Quart. Rev. Biol. 36:64–73.

Bang, B. G., and S. Cobb. 1968. The size of the olfactory bulb in 108 species of birds Auk 85: 55–61.

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

Bent, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds and their allies. U. S. Nat. Mus. Bull. 176.

Blough, D. S. 1957. Spectral sensitivity in the pigeon. J. Opt. Soc. Am. 47:827–833.

Cameron, A. T. 1947. The relative sweetness of sugars. Sugar Res. Found., Sci. Report Ser. 9.

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

Donner, K. O. 1960. On the effect of coloured oil droplets on the spectral sensitivity of the avian retina. Proc. XII. Int. Ornithol. Congr. 167–172.

Duncan, C. J. 1960. Preference tests and the sense of taste of the feral pigeon. Anim. Behav. 8:54–60.

Faegri, K, and L. van der Pijl. 1966. The principles of pollination ecology. Pergamon Press, Oxford.

Grant, K. A., and V. Grant. 1967. Effects of hummingbird migration on the California flora. Evolution 21:457–465.

Grant, K. A., and V. Grant. 1968. Hummingbirds and their flowers. Columbia Univ. Press, N.Y.

Hainsworth, F. R. 1974. Food quality and foraging efficiency: the efficiency of sugar assimilation by hummingbirds. J. Comp. Physiol. 88: 425–431.

Hainsworth, F. R., and L. L. Wolf. 1972a. Crop volume, nectar concentration, and hummingbird energetics. Comp. Biochem. Physiol. 42:359–366.

Hainsworth, F. R., and L. L. Wolf. 1972b. Power for hovering flight in relation to body size in hummingbirds. Am. Nat. 106:589–596.

Hartman, F. A., and K. A. Brownell. 1959. Liver lipids in hummingbirds. Condor 61:273–279.

Honigman, H. 1921. Untersuchungen über Lichtempfindlichkeit und Adaptierung des Vogelauges. Pflüg. ges. Physiol. 189:1–72.

Ikeda, H. 1965. The spectral sensitivity of the pigeon (*Columba livia*). Vision Res. 5:19–36.

Kare, M. R., and W. Medway. 1959. Discrimination between carbohydrates by the fowl. Poultry Sci. 38:1119–1126.

Lasiewski, R. C. 1962. The capture and maintenance of hummingbirds for experimental purposes. Avic. Mag. 68:59–64.

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

Norris, K. S. 1967. Color adaptation in desert reptiles and its thermal relationships. p. 162–229. *In* Lizard ecology: A symposium. Univ. of Missouri Press, Columbia, Mo.

Officer, H. R. 1964. Australian honeyeaters. Bird Observers Club, Melbourne.

Ortiz-Crespo, F. I. 1967. Interactions of 3 sympatric species of California hummingbirds in a planted area containing melliferous flowering vegetation. MS Thesis, Univ. California, Berkeley.

Pearson, O. P. 1954. The daily energy requirements of a wild Anna Hummingbird. Condor 56:317–322.

Percival, M. S. 1961. Types of nectar in angiosperms. New Phytol. 60:235–281.

Percival, M. S. 1965. Floral biology. Pergamon Press, Oxford.

Porter, W. P. 1967. Solar radiation through the living body walls of vertebrates with emphasis on desert reptiles. Ecol. Monogr. 37:273–296.

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

Ruschi, A. 1953. A cor preferida pelos beija-flores, e a porcentágem de açúcar preferida pelos mesmos. Bol. Mus. Biol. "Mello-Leitão" 22:1–5.

Skead, C. J. 1967. The sunbirds of southern Africa. Cape & Transvaal Printers, Cape Town.

Slud, P. 1960. The birds of Finca "La Selva", a tropical wet forest locality. Bull. Am. Mus. Nat. Hist. 121:49–148.

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

Stiles, F. G. 1973. Food supply and the annual cycles of the Anna Hummingbird. Univ. California Publ. Zool. 97:1–116.

Stiles, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rica *Heliconia*. Ecology 56:285–301.

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

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

Van Riper, W. 1960. Does a hummingbird find nectar through its sense of smell? Sci. Am. 202: 157 & ff.

von Frisch, K. 1950. Bees: their vision, chemical senses, and language. Cornell Univ. Press, Ithaca, N.Y.

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

Wolf, L. L. 1969. Female territoriality in a tropical hummingbird. Auk 86:490–504.

Wolf, L. L., and F. R. Hainsworth. 1971. Time and energy budgets of territorial hummingbirds. Ecology 52:980–988.

Wolf, L. L., F. R. Hainsworth, and F. G. Stiles. 1972. Energetics of foraging: rate and efficiency of nectar extraction by hummingbirds. Science 176:1351–1352.

Wolf, L. L., and F. G. Stiles. 1970. Evolution of pair cooperation in a tropical hummingbird. Evolution 24:774–789.

Departmento de Biología, Universidad de Costa Rica, Costa Rica, America Central. Accepted for publication 3 July 1974.