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RUFOUS HUMMINGBIRD SUCROSE PREFERENCE: PRECISION OF SELECTION VARIES WITH CONCENTRATION[1]

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Abstract. We tested concentration preferences of Rufous Hummingbirds (*Selasphorus rufus*) offered sucrose solutions in small feeders in the field. When sucrose solutions differing in increments of 10%, from 10% to 70%, were presented simultaneously, hummingbirds preferred 50% to higher and lower concentrations. They did not show a significant preference in the range from 50% to 70% . When options were offered in pairs of choices differing from 1–25%, hummingbirds demonstrated statistically significant preferences that varied with mean concentration in a curvilinear manner. At concentrations approximating those of hummingbird-pollinated flowers (20%), hummingbirds showed greatest specificity and could distinguish solutions differing by only 1%. At concentrations above and below 20%, greater differences between choices were required to elicit significant preferences.

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Key words: Rufous Hummingbird, Selasphorus rufus, *sugar preference.*

The ability of hummingbirds to choose optimal sugar sources is of obvious adaptive significance to their survival, migration, and reproduction. Previous studies suggested that Rufous Hummingbirds (*Selasphorus rufus*) prefer relatively high sucrose concentrations, up to 60%, when presented concentration options differing by 10% or more (Roberts 1996, Blem et al. 1997). However, lick volumes and licking rates decrease with increased nectar concentration (Kingsolver and Daniel 1983, Roberts 1995), resulting in higher energy-intake rates at 25–35% than at higher concentrations. Hummingbird feeding preferences may be influenced by flower color (Stiles 1976, Miller et al. 1985), flower position (Miller et al. 1985), sugar composition (Martinez del Rio 1990), viscosity of nectar (Stromberg and Johnsen 1990), nectar secretion rate (Pyke and Waser 1981, Gill 1988, Stiles and Freeman 1993), and the fit of the bird's bill within the flower's corolla (Stiles

TABLE 1. F-values for ANOVA of simultaneous effects of feeder location and direction, trial sequence (repeated measures), and concentration of sucrose solution on significance of difference between two choices offered simultaneously.

Mean concentration	Choices (%)[a]		F-values			
			Site	Direction	Trial	Concentration
10%	7.0	13.0	1.7	2.1	0.0	28.7***
10%	7.5	12.5	3.6*	2.4	5.1*	147.9***
10%	8.0	12.0	15.5***	2.9*	6.9*	0.6
20%	19.0	21.0	3.3*	0.7	4.9*	4.5*
20%	19.5	20.5	1.0	1.8	27.6***	5.9*
30%	28.5	31.5	2.5	0.7	2.3	9.5**
30%	29.0	31.0	27.1***	3.1*	31.5***	3.2
30%	29.5	30.5	3.1*	1.2	16.5***	0.3
40%	36.5	43.5	3.4*	0.3	85.1***	9.8***
40%	37.0	43.0	14.5***	2.6	0.1	2.3
40%	38.0	42.0	17.9***	8.1**	9.0***	0.7
50%	44.0	56.0	20.7***	0.8	6.9**	6.3**
50%	44.5	55.5	1.4	0.8	0.6	3.4
50%	45.0	55.0	11.4***	0.5	62.4***	0.0
50%	46.0	54.0	20.2***	0.3	65.8***	0.0
60%	45.0	75.0	5.1*	1.1	1.0	13.6***
60%	47.0	73.0	8.2**	3.9	3.8	24.1***
60%	47.5	72.5	10.0**	1.9	4.0	4.5*
60%	48.0	72.0	14.0***	1.8	61.3***	1.3
60%	50.0	70.0	18.3***	0.8	25.7***	1.5

[a] Choices (%) refers to the two levels of sucrose simultaneously available during a given test.
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

1975). Test conditions such as trial sequence, site of tests, and direction of the feeders also could influence results. Holding most of these variables constant is necessary in order to determine the resolution at which hummingbirds discriminate between concentrations. In the present study, we measured preferential selection by Rufous Hummingbirds of sucrose solutions differing by 1–25% provided in small (10 ml) feeders placed in natural field sites. Specifically, we asked the question: How precisely do hummingbirds select sucrose solutions over a range of concentrations?

METHODS

We studied hummingbirds from 4 June through 5 August, 1996, and 30 June through 31 July, 1997, at Flathead Lake Biological Station in Lake County, Montana (47°53′N, 114°02′W; altitude 890 m). We performed preference tests at 12 stations at 100-m intervals along a transect established at the edge of the forest. At each station we placed a 2-m pole to which we attached four 10-ml plastic syringes (graduated at 0.1 ml intervals), directed in the cardinal directions: (0°, 90°, 180°, and 270°). Tips of the syringes were painted fluorescent orange to attract hummingbirds and directed upward to prevent dripping. In all tests of preference, different concentrations were arranged so that each was present equally at all directions. The position of various concentrations and the order of tests were randomized. All solutions were made up as mass/volume percentages, where a 40% solution is 40 g of sucrose in 100 ml of water (Stromberg and Johnsen 1990). The arrangement of solutions was changed in replicate tests, but equal representation of concentrations was maintained throughout. All tests were run for 2–4-hr periods from 9:00 to 19:00. We visited the sites approximately every hour and recorded the level of sucrose in each syringe. We never allowed sucrose levels to drop more than 1 cm from the syringe tip, because hummingbirds shifted to secondary preferences when the most preferred solution was depleted beyond the bird's reach (usually > 2 cm).

Two groups of tests were run. In the first, we tested sucrose preference by simultaneously providing four concentrations differing by 10%. Four separate tests were performed spanning a total range of concentrations from 10 to 70%. In the second test, we tested sugar preference using pairs of sucrose solutions differing equally above and below mean concentrations of 10, 20, 30, 40, 50, and 60% (Table 1). Each concentration was represented twice at each pole at cardinal directions chosen so that concentrations were presented in equal numbers at all directions. We began tests at a given concentration by presenting two choices differing by 4–6%. If a significant preference was obtained, we then reduced the differences between choices in the next tests until a nonsignificant result was obtained. If the difference was not significant, we increased the difference, usually by 1–2%, until a significant difference was obtained (Table 1). Additional tests were done in order to determine the level of preference to the nearest 1%. Each of these tests was done simultaneously at six sites on two different days. Sample sizes always were 48 (2 concentrations × 2 directions × 6 sites × 2 days). Control vials containing identical solutions were used in each test. These were fitted with screen collars, which excluded hummingbirds, but not ants or bees. During the course of any single test these did not lose a measurable amount of fluid, therefore no corrections were made for evaporation or other loss.

None of the measurements of sucrose consumption (ml) deviated significantly from a normal distribution (SAS 1990, Proc Univariate). In order to control for impact of extraneous independent variables on sucrose preference, we tested for significant effects of direction, test site, test sequence (differences between repetitions), and solution concentration by repeated measures analysis of variance (SAS 1990, Proc GLM). Differences in preference were judged to be significant only when all other variables were first controlled by the model and sucrose concentration provided a significant F-value (type III sum of squares). All P-values less than 0.05 were considered to be statistically significant.

RESULTS

In the first studies, when sucrose solutions were offered to hummingbirds at four concentrations differing by 10%, they demonstrated significant differences among all concentrations offered from 10–50%. Above 50%, differences in preferences began to disappear. Hummingbirds never showed a preference between 50% and 60%, or 50% vs. 70%.

In the second set of tests, we focused on the smallest detectable differences around each of the concentrations tested in the first studies. In most trials there were significant differences among test sites and trial order. In a few tests, there also was a significant difference among directions of the opening of the feeder (Table 1). However, when type III sum of squares were computed (SAS 1990), the results indicated that hummingbirds were able to detect differences as small as 1% in sucrose concentrations when tested at mean concentrations near that of hummingbird flowers (Table 1). The greatest precision was at concentrations near 20% sucrose. As concentrations were increased, the differences necessary to cause statistically significant preferences increased in a curvilinear fashion (Fig. 1).

DISCUSSION

For decades, one of the centerpieces of foraging theory has been the hypothesis that much of bird behavior is directed toward maximizing energy acquisition. Studies of hummingbird feeding generally have supported this hypothesis (Montgomerie et al. 1984, Tamm and Gass 1986). Available energy reserves in flowers vary substantially. Nectar concentrations of flowers can range from 8 to 43% sucrose (Hainesworth 1973), and concentrations sometimes vary with time of day and with variations in environmental conditions (Plowright 1981, Bertsch 1983). Because flowers differ significantly in sugar concentration, we hypothesized that hummingbirds should be able to distinguish between small differences in nectar concentrations when the amount of solution was constant. Sugar concentrations of bee-pollinated flowers regularly exceed 35%, but hummingbird-pollinated flowers have more dilute nectars of 20–25% (Baker 1975, Bolten et al. 1979). Heyneman (1983) predicted that for large nectar sources, hummingbirds would have optimal energy uptake at concentrations of 22–26% sucrose. It therefore is logical that greater ability to discriminate should occur in the lower range. The present study indicated that hummingbird preferences are most precise in the range of the flowers they most often exploit for nectar and, therefore, supports our hypothesis. However, there also may be considerable variation among secretion rates and amount of nectars of hummingbird-pollinated flowers (Stiles and Freeman 1993), and amount of nectar secreted may be more variable than concentration. The relationship between availability of total energy reserves and hummingbird visitation rates may need more scrutiny.

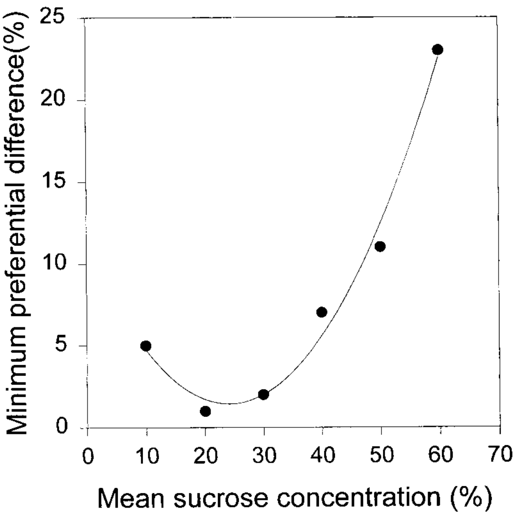

FIGURE 1. Minimum preferential differences of Rufous Hummingbirds for sucrose as a function of mean sucrose concentrations offered.

We do not contend that the present study represents natural foraging behavior in hummingbirds. The amount of nectar and the higher concentrations are generally unlike those found in flowers. However, this experiment was designed to determine the precision with which hummingbirds could distinguish different concentrations under field conditions. "Preference" is defined as priority of choice and implies that more than one option is available. Therefore, when one makes statements about preference, they are only valid in the context of the range of choices at hand. For example, in laboratory tests, Roberts (1996) presented Rufous Hummingbirds with 1-μl containers of sucrose solution in 10 pair-wise combinations in 10% increments from 25% to 65%. These feeders were refilled only when birds left, therefore yielding only 1-μl per visit, and thus simulated flowers more closely than the present study. However, the results of Roberts' study were similar to ours, suggesting that volume of nectar used in each experiment had little or no effect on concentration preference. That is not to say that volume is not important. It perhaps is the most important variable in the field because hummingbirds would benefit from large, reliable nectar sources.

In previous preference tests, hummingbirds typically have chosen high concentrations of artificial sugar solutions, sometimes 45–65% (Roberts 1996, Blem et al. 1997). Neither hummingbird preferences nor energetic considerations account for the low concentrations of sugar in flowers they visit (Roberts 1996). The present study differs from numerous other investigations of hummingbird sugar preference in at least two important ways. First, most preference studies have been conducted in the laboratory (Roberts 1996). Second, other studies have tested preferences between relatively great sugar concentrations (Stiles 1976, Tamm and Gass 1986, Blem et al. 1997). We are not aware of any study that has used an approach near that of natural conditions, i.e., sugar levels approximating those of hummingbird-pollinated flowers presented in the field. Furthermore, our study approximates laboratory conditions in two important aspects: (1) amount of sugar is unlimited and (2) there are no constraints of flower morphology. One must be cautious in generalizing about natural behavior of hummingbirds from all such studies.

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