J. Field Ornithol., 68(2):245–252

FIELD STUDIES OF RUFOUS HUMMINGBIRD SUCROSE PREFERENCE: DOES SOURCE HEIGHT AFFECT TEST RESULTS?

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Abstract.—Several environmental factors affect hummingbirds' selection of sugar sources. Using a factorial test design that included several different sucrose concentrations, source heights, and test locations, we measured amounts of sugar solution that Rufous Hummingbirds (*Selasphorus rufus*) removed from small (10 ml) feeders placed in successional habitat around old-growth forest. Hummingbirds showed statistically significant preferences for increasing sucrose concentrations from 20% up to, but not including 70% sucrose (by mass-volume). Height significantly affected preference under nearly all conditions. Hummingbird usually preferred elevated sources over those near the ground. In some instances there were differences in preference between test locations, possibly because of differing numbers of hummingbirds visiting sucrose sources.

ESTUDIOS DE CAMPO SOBRE LAS PREFERENCIAS DE SUCROSA POR PARTE DE *SELASPHORUS RUFUS*: AFECTA LOS RESULTADOS LA ALTURA DE LA FUENTE DE ALIMENTOS?

Sinopsis.—Varios factores ambientales afectan la selección de fuentes de azucar por parte de zumbadores. Utilizando un diseño de prueba factorial, que incluyó diferentes concentraciones de azucar, fuentes del recurso, altura y localización de la prueba, medimos la cantidad de azucar que *Selasphorus rufus* removían de libadores de 10 ml. El trabajo se llevó a cabo en un habitat sucesional en los alrededores de un bosque maduro. Los zumbadores mostraron una preferencia significativa en el incremento de la concentración de sucrosa desde 20% en adelante, sin incluir la comcentración de 70% (peso por volumen). La altura en que se colocaron los libadores afecto significativamente la preferencia de utilización, virtualmente, bajo cualquier condición. Los zumbadores prefirieron fuentes de alimentos elevadas sobre aquellas cerca del suelo. En algunas ocasiones hubo diferencias en preferencias entre las localidades de prueba, debido, posiblemente, al número diferente de zumbadores que visitaron las fuentes de sucrosa.

There have been numerous studies of hummingbird feeding ecology, but the majority of these have been largely or completely theoretical or were done in laboratory settings. Few empirical analyses of hummingbird nectar preference under field conditions have been attempted. Hummingbirds are specialized nectar-feeders (Stiles 1981) and are capable of absorbing and digesting a variety of sugars. However, they often show a preference for more complex sugars, particularly sucrose (Martinez del Rio 1990). Hummingbirds prefer highest available sucrose concentrations (up to 60%; Stiles 1976) over simple sugars, artificial sweeteners (Stromberg and Johnsen 1990), and lower concentrations of sucrose. Previous studies also predict that hummingbirds would have optimal energy intakes when feeding on 22–26% (Heyneman 1983) or 35–40% sucrose solutions

(Kingsolver and Daniel 1983). The effect of height of sugar source on sugar preference seems not to have been studied.

The present study analyzes the degree to which sugar concentration and height of sugar source affects hummingbird nectar preference. The hummingbird involved in all of our tests, the Rufous Hummingbird (*Selasphorus rufus*), has not been tested with regard to its food preferences, although its foraging ecology has been thoroughly studied (e.g., Carpenter et al. 1993, Heinemann 1992, Temeles and Roberts 1993). We specifically ask the questions: (1) Does sucrose concentration affect Rufous Hummingbird sugar selection in the field?, (2) What is the maximum sucrose concentration that these hummingbirds will ingest?, and (3) Does height and location of the sucrose sources affect selection and degree of use?

STUDY AREA AND METHODS

We studied hummingbirds from 10 Jun.–2 Aug. 1995, at Flathead Lake Biological Station in Lake County, Montana (47°53′N, 114°02′W; altitude 890 m). Both Rufous Hummingbirds and Calliope Hummingbirds (*Stellula calliope*) occurred in the study area, although the former was much more abundant during our study. The station included a 20-ha stand of old-growth forest composed of Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), western larch (*Larix occidentalis*), and ponderosa pine (*Pinus ponderosa*). Successional vegetation surrounded the buildings of the station along with scattered, large trees of the species listed above. We performed preference tests at several locations along edges of successional habitat. Each test station was more than 100 m from the others. Common flowering plants near the test sites were ocean spray (*Holodiscus discolor*), woods rose (*Rosa woodsi*), mock orange (*Philadelphis lewisii*), and snowberry (*Symphoricarpus albus*). These were all commonly used by hummingbirds and all were less than 2 m high.

We used 10-ml scintillation vials (73 × 20 mm diameter), graduated at 0.1-ml intervals to test hummingbird preference for sucrose. Three vials were attached to a 2.5-m pole, one each at 1.25, 1.63, and 2.0 m from the ground. Each test site consisted of three such poles in a line at 25-cm intervals. This produced a three × three grid of vials over a vertical plane of 0.75 × 0.75 m. The vials had fluorescent orange (Krylon 522) caps with central holes 8 mm in diameter through which hummingbirds could sample solutions from the top. Tests were initiated by filling all vials with sucrose solution. Such feeders do not present the sugar solution in the same manner as in a flower, provide sugar in large quantities relative to flowers, and result in modification of the natural foraging behavior observed when hummingbirds visit flowers. Nevertheless, birds typically tested all vials in an individual station, and then generally concentrated their foraging on single vials. In all tests of preference, three different concentrations were arranged so that each concentration was present at all three heights and randomly placed to left, right, or center. All solutions were made up as mass/volume percentages, where a 40% solution

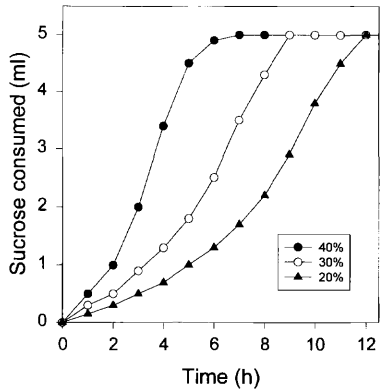

FIGURE 1. Timing of sucrose consumption by Rufous Hummingbirds feeding at stations providing 20, 30, and 40% sucrose in individual vials (points are means of eight feeders).

was 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 started at 0800 h MST. We visited the sites approximately every hour and recorded the level of sucrose in each vial. In preliminary tests we noted that hummingbirds shifted to secondary preferences when the most preferred solution was depleted in the vial beyond the bird's reach (Fig. 1). We therefore ended each test when levels of solution in preferred vials reached 4.5–5.0 ml, the maximum distance we observed them reaching. This protocol generally required 5–8 h to complete and allowed us to determine which samples were chosen most intensively at first. When tests were allowed to continue past this point, hummingbirds switched to less-preferred concentrations and all solutions eventually were depleted (see Fig. 1). We watched vials periodically throughout the tests and recorded the number of visits by hummingbirds. Small variations in plumage, visible at close range through 8 × 35 binoculars, were used to recognize individual birds.

In our first set of experiments we tested sugar concentration preference using several combinations of sucrose solutions (Table 1). These were 20, 30, and 40%; 30, 40, and 50%; 40, 50, and 60%; and 50, 60, and 70% sucrose (henceforth expressed as 20/30/40, 30/40/50, 40/50/60, and 50/60/70). Each of these tests was done at four sites on two different days for a total of eight tests for each group of concentrations. Tests using 20/30/40 were run on consecutive days. Experiments using higher concentrations were alternated with each other. The 20/30/40 tests were repeated a second time at the end of July and early in August. Sample sizes always were 72 (3 concentrations × 3 heights × 4 sites × 2 days).

Additional control vials containing identical solutions were used in each test to determine amounts of sugar solution lost to evaporation and insects. These vials were fitted with screen collars which excluded humming-

TABLE 1. Hummingbird consumption (percentage of maximum) from test vials at Flathead Lake Biological Station, Montana. All values are means ± 1 SE. Concentrations of sucrose are in g/100 ml (n = 8 for all means).

Height (m)	Concentration		
	20%	30%	40%
2.00	28.1 ± 3.0	70.1 ± 7.0	88.9 ± 2.7
1.63	20.3 ± 1.2	61.1 ± 9.7	74.5 ± 5.3
1.25	22.2 ± 1.6	67.2 ± 7.4	86.6 ± 3.3
	30%	40%	50%
2.00	79.6 ± 4.5	85.3 ± 4.1	85.8 ± 3.6
1.63	61.6 ± 3.2	79.7 ± 5.9	83.4 ± 4.2
1.25	70.6 ± 5.4	77.9 ± 9.3	80.4 ± 3.6
	40%	50%	60%
2.00	57.6 ± 8.3	65.0 ± 7.5	73.6 ± 9.6
1.63	44.5 ± 6.2	55.2 ± 5.0	72.3 ± 7.6
1.25	44.1 ± 7.4	52.9 ± 9.1	59.9 ± 7.6
	50%	60%	70%
2.00	55.4 ± 6.7	59.3 ± 9.8	77.7 ± 7.7
1.63	37.4 ± 8.8	53.4 ± 9.9	53.6 ± 9.9
1.25	52.6 ± 9.9	56.0 ± 9.8	60.4 ± 9.6

birds, but not ants, bees, or other insects. During the course of any single test these did not lose a measurable amount of fluid, therefore no corrections were made. Tests were not done in a particular sequence and all except 20/30/40 tests were run alternately with each other. The 20/30/40 tests were repeated a second time at the end of July and early in August.

In a second set of experiments we specifically tested the effect of height on preference. We attached 12 vials at 25-cm intervals (form 25 cm to 3 m) to individual 3-m poles. All vials were filled with 40% sucrose solutions and all other methods were as described above, except that single 3-m tests were performed at seven different sites (12 vials × 7 sites).

We statistically tested significance of the simultaneous effects of height, test site, test sequence, and concentration of solution by analysis of variance (Proc Anova, SAS Institute 1990). Because the amount of solution removed by hummingbirds differed among test sites, we standardized raw measurements by converting them to percentages of the maximum removed from any single vial in the entire test. These percentages were then logarithmically transformed (Zar 1984) to increase their likelihood of being normally distributed. All transformed data sets did not deviate significantly from normality (Proc Univariate; SAS Institute 1990). ANOVA were then performed on these transformed data, using test location, sequence of test, height of vial, and sucrose concentration as independent variables. A P-value ≤ 0.05 was considered to be significant in all tests.

RESULTS

While we watched the vials (25 h), only 4 of 476 visits were by Calliope Hummingbirds. We also recorded a single visit by Anna's Hummingbird (*Calypte anna*). During June tests, sites were visited by as few as three dif-

TABLE 2. Results of analysis of variance of Rufous Hummingbird sucrose preference (n = 72 for each ANOVA) at Flathead Lake Biological Station, Montana.

Concentrations	Source of variation	F	P	r^2
20/30/40	Model	39.0	<0.0001	0.81
	Height	1.9	0.0317	
	Concentration	63.9	<0.0001	
	Site	2.7	0.0027	
30/40/50	Model	5.0	<0.0001	0.36
	Height	2.1	0.0488	
	Concentration	5.4	0.0002	
	Site	2.2	0.0299	
40/50/60	Model	4.0	0.0012	0.30
	Height	3.2	0.0496	
	Concentration	5.7	0.0044	
	Site	3.2	0.0290	
50/60/70	Model	7.9	<0.0001	0.46
	Height	2.9	0.0421	
	Concentration	2.7	0.0776	
	Site	14.7	<0.0001	

ferent hummingbirds, but later in July as many as six hummingbirds were seen feeding simultaneously at some sites. Only adult hummingbirds visited early in the tests, but measurements after mid-July included visits by both adults and recently fledged young. The latter typically visited in pairs and were recognizable by their behavior and plumage.

In all tests, except that using 50/60/70, Rufous Hummingbirds showed statistically significant preferences for greatest available sucrose concentrations (Tables 1 and 2). There was significant variation in sucrose selection among heights of the vials in every experiment. The preferred vials were those placed highest in the grid and most-preferred vials were those with highest concentrations at highest points. In every case we found significant differences in amount consumed among test sites (Table 2).

In tests with 40% sucrose presented at 0.25-m intervals from 0.25–3.0 m, height of vials ($F_{11,167}$ = 7.51; $P < 0.0001$; Fig. 2), and variation between stations ($F_{11,167}$ = 13.73) significantly affected preference, while order of the tests (time) did not ($F_{11,167}$ = 3.47; P = 0.07).

DISCUSSION

Most of the extensive literature on Rufous Hummingbirds deals with foraging behavior and energetics (Calder 1993). However, we are aware of few sugar preference studies conducted in the field, and these did not include features of habitat as variables. We do not find fault with the results of nonfield research of hummingbirds, but believe that studies in the more complex field environment may be illuminating in some regards.

Previous studies have indicated that hummingbird feeding behavior is affected by numerous factors (Martinez del Rio 1990, Stiles 1976, Stromberg and Johnsen 1990). For example, Stiles (1976) found that feeding

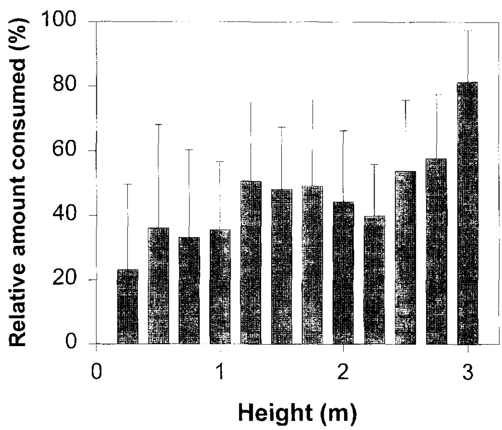

FIGURE 2. Consumption (% of maximum) of 40% sucrose from vials at 0.25–3.0 m ($\bar{x}$ ± 1 SE).

preferences in Anna's Hummingbirds were influenced by sugar concentration and color of nectar. Our measurements indicate that sugar concentration is influential when solutions are 60% sucrose or less. Preference was most distinctly shown in tests using lower amounts of sucrose. In tests in which all choices were 50% sucrose or greater, hummingbirds did not select for concentration, but height of the source remained statistically significant. We suspect that amount of sucrose removed is influenced secondarily by the surrounding vegetation, particularly presence and height of plants covering the forest floor, and the location of nests.

In previous studies, however, habitat features generally seem to have been overlooked. Hummingbirds learn preferences for food sources and it is likely that they transfer this process to artificial feeding stations (Brown and Gass 1993, Miller et al. 1985). It therefore is important to randomize positions of individual vials in station arrays, as done in the present study, and to change these positions between individual tests.

Rufous Hummingbirds occasionally foraged on flowers as low as 15 cm from the ground and as high as 10 m. The former was rare, however. We hypothesize that avoidance of low flowers may reduce risk of predation. The most common potential bird predators on the station are mammals, including the Columbian ground squirrel (*Citellus columbianus*), red squirrel (*Tamiasciurus hudsonicus*), and weasels (*Mustella frenata, M. erminea*). We have seen both squirrel species killing and eating small birds. With the possible exception of the Sharp-shinned Hawk (*Accipiter striatus*), there appear to be no avian predators that commonly take hummingbirds in this region and habitat (Miller and Gass 1985).

Preference was most distinctly shown in tests using lower amounts of sucrose. In tests in which all of the choices >50% sucrose or greater, hummingbirds apparently did not select for concentration, but height of the source remained statistically significant. Rufous Hummingbirds show a distinct preference for the highest sucrose sources, but presence of more than one bird complicates the pattern. Hummingbirds typically perched on the highest vial, on top of the supporting pole, or on nearby branches above the highest vial. Females typically came several hundred meters from nests to visit feeding stations. After the young fledged, females sometimes were accompanied by one or two immature birds, probably their offspring. In tests using 3-m poles there were preference peaks at about 0.5, 1.5 and 3.0 m (Fig. 2). This appeared to be the result of competitive interactions among birds feeding simultaneously at each station. Dominant individuals (often males) typically sat on the top vial or tip of the pole and drove other birds to lower levels. This sometimes was repeated a second time by the birds at middle vials, so that three birds were partitioning the entire sampling station. Each bird appeared to be using (and defending) the highest source to which it had relatively free access.

Future tests should be performed using single vials at different heights at separate stations so as to reduce the effect of competitive interactions. Preference for highest vials in such tests would be indicative of the general advantage of high vantage points in watching for predators and competitors. The present study indicates, at least superficially, the potential complexity of the factors influencing probability of flower visitation by hummingbirds. Next generation models testing hummingbird preferences will investigate this complexity more completely.

ACKNOWLEDGMENTS

We are indebted to the members of the Ecology of Birds class at Flathead Lake Biological Station, 1995, for their help in completing tests, suggestions for improving the procedures, and discussions about sucrose preferences in hummingbirds. The manuscript benefited greatly from revisions suggested by Sara Hiebert and C. Ray Chandler.

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Received 17 Apr. 1996; accepted 22 Jul. 1996.