

## HUMMINGBIRD SWEETNESS PREFERENCES: TASTE OR VISCOSITY?<sup>1</sup>

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*Abstract.* Black-chinned Hummingbirds (*Archilochus alexanderi*) were offered combinations of sucrose and artificial sweeteners (saccharin, aspartame) at various concentrations and viscosity levels. Sucrose at 40% concentration was preferred over lower concentrations. Sucrose at 20% was preferred over artificial sweeteners, plain water, and low sucrose/high viscosity samples. Additions of artificial sweeteners to sucrose samples had no effect on nectar consumption and, therefore, were judged to be ineffective stimuli rather than aversive. Artificial increases in viscosity had no effects on the amount of nectar removed as long as a minimum of 15% sucrose was present. Hummingbirds responded to decreased sucrose concentrations by increasing sampling behavior at feeders; at increased sucrose levels, sampling behavior decreased. Chemosensory mechanisms rather than physical measures of viscosity are responsible for the sensory evaluation and the subsequent selection of sucrose nectars.

*Key words:* Black-chinned hummingbird; taste; sucrose; viscosity; sweeteners; chemosensory.

### INTRODUCTION

Stiles (1976) observed that feeding behavior in Anna's Hummingbird (*Calypte anna*) followed a hierarchy of preferences based on (1) energetic content, (2) sugar concentration, (3) taste, and (4) color of the nectar offered in samples on artificial feeders. Stiles also demonstrated that the highest available sucrose concentration (up to 60%) was preferred although the birds may be less efficient at metabolizing these solutions. Kingsolver and Daniel (1983) predicted that hummingbirds feeding on large volume nectar sources would have an optimal energy intake consuming 35-40% sucrose solutions. This prediction was based on biomechanical considerations involving the viscosity of the fluid, morphology of the bird's tongue and bill, and its licking behavior. Heyneman (1983) predicted that for similar large volume nectar sources, hum-

mingbirds would have an optimal energy uptake based on nectar of 22-26% sucrose. This prediction was based on the emphasis of nectar uptake limits due to increased viscosity. However, the sensory basis for nectar selection by hummingbirds remains largely unexplored (Scogin 1985) and it is not known whether hummingbirds show behavioral response to nectars based on sucrose receptors, by sweetness receptors, or by a physical measure of viscosity.

We examined the independent effects of sweeteners and viscosity on the feeding responses of Black-chinned Hummingbirds (*Archilochus alexanderi*) by using combinations of sucrose, artificial sweeteners, and agents that affect viscosity. We also investigated whether nectar selection by hummingbirds showed a hierarchy based on viscosity or sweetness.

### STUDY AREA AND METHODS

Black-chinned Hummingbirds are the only breeding hummingbird on the study site, National Audubon's Research Ranch (Strong 1987). The site is located on the northwestern side of the Huachuca Mountains in Santa Cruz County, Arizona and includes rolling foothill grassland

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and oak savanna at elevations from 1,400 to 1,560 m. Mean precipitation is 43 cm/year, with most of this falling in thunderstorms in July, August, and early September. Grasses, dominated by various grama grasses (*Bouteloua* spp.) occur in a savanna with Emory oak (*Quercus emoryi*) and Arizona white oak (*Q. arizonica*). For more detailed descriptions of the study site, see Bahre (1977), Bock et al. (1984), Bock and Bock (1986), and Brady et al. (1989).

Free-ranging birds were attracted to a series of 10 Droll Yankee Disk feeders arranged in shade under open canopies of Emory oaks scattered 300 m along a ridge. In a preliminary series of experiments, feeders were moved until roughly even use of each feeder was observed. Subsequently, feeder locations were not changed for the duration of the study. Each feeder had three, bright red, plastic artificial flowers with small "corolla tubes" (3 mm inside diameter), which provided more than adequate room for birds to extend their beaks through and into a 250-ml reservoir below. The main body of the feeder was translucent green plastic. Each artificial corolla disk and attached corolla tube could be described as "rotate" (Harrington and Durrell 1957) or "rotate to salverform" (Hickman 1989, p. 22). Nectar in the reservoir did not touch the artificial corollas. Feeders were filled daily with 20% sucrose solution and birds had access to the large reservoir in each feeder during the study period—May to August 1986 and May to July 1987. When experiments were conducted, feeders and/or nectar were briefly modified. For presentations of test nectars, each plastic corolla was removed from the feeder's main reservoir and inserted into a 0.5-ml disposable centrifuge tube. Centrifuge tubes with the attached artificial corollas were returned to the holes on feeder reservoirs which usually held only the plastic corollas. Thus, the birds, instead of drinking from the open reservoir, drank by inserting their bills through the artificial corollas (as usual) but took fluid only from an individual centrifuge tube with a test nectar.

Centrifuge tubes were filled with a test solution, capped, and weighed in the laboratory. At each feeder, we opened the tubes and placed them under the plastic corollas on feeders. We watched feeders with binoculars from a distance of at least 5 m. When slightly more than half of the nectar was consumed, all tubes were removed from the feeders and sealed again. Birds required 15–30

min to drink this much nectar. To determine the amount of test nectar consumed, tubes were again capped, transported to the laboratory, and weighed to the nearest 0.01 g. No evaporation losses were observed in control tubes.

Solutions are expressed as weight/volume; 25% sucrose is 25 g sucrose in 100 ml of water. Deionized, distilled water was used in all solutions. We used "Equal" at the manufacturer's reported equivalency of 0.5 g Equal to one teaspoon of sucrose (mean weight of level teaspoon of sucrose was 4.10 g,  $n = 20$ ,  $SD = 0.123$ ). Equal contains dextrose, dried corn syrup, aspartame, silicone dioxide, cellulose, and tribasic calcium phosphate. Pure aspartame (G. D. Searle, Skokie, Illinois) is 200 times as sweet as sucrose (see Homler 1984, Newsome 1986) so equivalent solutions to 20% sucrose were made with 0.1 g aspartame/100 ml water. In humans, solutions with concentrations of 0.033 g saccharin/100 ml water approximate the sweetness of 20% sucrose solutions (Carol M. Christensen, pers. comm.).

We increased the viscosity of solutions with sodium carboxy methyl cellulose CMC (7MF, Hercules Corp. Wilmington, Delaware). CMC was added slowly to water and stirred for several hours. Viscosity measurements were made with Cannon-Ubbelohde four bulb shear dilution capillary viscometers (Model S122, Cannon Instrument, State College, Pennsylvania) following Christensen (1980). Viscosity was measured at ambient temperatures of the study site. The relationship between sucrose concentration,  $x$  (g/100 ml), and viscosity,  $y$ , (centistokes) was determined by regression ( $R^2 = 0.993$ ,  $df = 16$ ,  $P < 0.001$ ) and can be described as  $y = 0.896 + 0.017x + 8.049 E - 4x^2$ . The relationship between CMC concentration,  $m$  (g/100 ml), and viscosity was determined by regression ( $R^2 = 0.999$ ,  $df = 24$ ,  $P < 0.001$ ) and can be described by  $y = 1.037 + 0.716 m + 0.77 m^2$ . Because nectar densities were near 1.0, viscosity expressed in units of centistokes is virtually identical to viscosity expressed as centipoise. Mixtures of sucrose and CMC solutions were not measured; viscosity values for the combinations do not add directly but rather follow a complex empirically derived function. Mixtures of sucrose and CMC were clearly more viscous than either alone.

Eleven birds were caught and given temporary paint markings. Using repeat observations as recaptures relative to the number of birds present

at any given time, a Lincoln-Petersen estimate of population indicated that about 100 birds were using the feeders in July 1987. Marked birds were observed as far away as 2 km from feeders. Overall numbers of hummingbirds at the study site did not vary markedly during the study periods. These birds have a bill and tongue morphology which is similar to that reported by Kingsolver and Daniel (1983) for Anna's Hummingbird (specimens examined, Museum Vertebrate Zoology). Internal grooves and bill shape were used in the contrasting models predicting optimal energy uptake (Kingsolver and Daniel 1983, Heyneman 1983).

Friedman's nonparametric two-way analysis of variance was used to compare differences in selection of nectars (Sokal and Rohlf 1981, p. 446; Siegel 1956, p. 166). For these tests, we present the associated chi square values. Each feeder was treated as one factor because the amount of nectar removed varied between feeder sites. We also present a parametric analysis of variance with associated *F*-values (Sokal and Rohlf 1981). Levels of significance for rejection or acceptance of null hypotheses were in all cases the same with either statistic. Each feeder replicated all the choices of test nectar offered during a particular trial. Test solutions were randomly assigned to each of the three locations on each feeder. Data compared were grams of nectar removed by hummingbirds from each feeder for each test nectar.

In some preliminary experiments, sucrose concentrations in feeder reservoirs were varied to determine if birds sampled several corollas and changed this behavior in response to changes in sucrose concentrations. Birds were allowed to visit unmodified feeders with a given nectar for as long as 7 days to establish a background or "before" condition. In this experiment, all artificial flowers lead to the single nectar reservoir on each feeder. Individual birds were observed as they approached from a distance to the ridge-top feeder stations and were followed until they departed the site. Behaviors that we counted during one visit by a hummingbird to the site included the number of corollas visited and the number of feeders visited while an individual bird was in the group of 10 feeders. We then changed sucrose concentrations in all feeders early one morning and repeated the observations of individual feeding bouts as the birds first encountered the altered nectar. Observations were

made each morning for up to 3 days after the changes in nectars were made. Goodness-of-fit statistics were calculated (Sokal and Rohlf 1981, p. 705) to compare changes in the distribution of numbers of recorded behaviors observed before and after sucrose concentrations were changed.

Calder (1979) suggested that water balance needs of hummingbirds could affect their nectar selection. However, the study site had open water available at all times in nearby stock watering ponds and in O'Donnell Creek. From May to July, air temperatures reach seasonal maxima and relative humidities reach minima (unpublished weather records on file at sanctuary). In August, almost daily rainfall increases water availability and flowers become abundant. Most observations were made between mid-morning and mid-afternoon.

## RESULTS AND DISCUSSION

### EXPLORATION BEHAVIOR

Most flowers used by hummingbirds have natural sucrose concentrations of about 20% (Baker and Baker 1975, Stiles 1976, Brown and Kodric-Brown 1979, Pyke and Waser 1981, Heyneman 1983, Waser 1983). When the hummingbirds were accustomed to 20% sucrose in the feeders, exploration behavior at each feeder often included visits to more than one corolla and more than one feeder (Table 1). When the sucrose concentration was increased to 40%, a significant reduction in exploration was evident; generally, birds stayed at one corolla and then flew off without visiting other feeders (Table 1). By the second day, the birds returned to the former pattern of sampling more than one corolla and more than one feeder (Table 1). Later we offered 30% sucrose in the feeders for several days. The hummingbird's corolla sampling pattern with 30% sucrose was not significantly different from the pattern with 20% sucrose ( $\chi^2 = 0.43$ ,  $P > 0.80$ ). When the energetic value of the nectar was dropped to 10% from 30%, the hummingbirds significantly increased searching, visiting both more corollas on each feeder and more feeders (Table 1). Because the drinking response of the hummingbirds was associated with measurable changes in sucrose content of nectars offered, we used drinking behavior by hummingbirds as a measure of their ability to discriminate between nectars. Responses of hummingbirds to the vary-

TABLE 1. Effects of changing sucrose concentrations on exploratory behavior of Black-chinned Hummingbirds. Statistical comparisons are between the distributions of numbers of corollas visited (A) or number of different feeders visited (B) by hummingbirds on days 1–3 and respective distributions on subsequent days. One observation was obtained by focusing on an individual bird from the time it came into view as it approached the string of feeders to the time the bird could no longer be seen as it left the locality of the feeders. Sucrose nectar (20%) was provided ad libitum in a string of 10 feeders for several weeks before the experiment. Sucrose concentrations in the feeders were first raised from 20% to 40%. Observations were taken during early morning hours several days before this change and during the first 3 days after this change. Then all feeders were maintained for 7 days with sucrose nectar at 30%. Observations were taken during early morning hours for 3 days with the 30% nectar and on the morning that the nectar concentration was dropped to 10%. Birds did not visit more than two feeders before leaving the location of the feeders. "Total" indicates number of observations. Abbreviations: \*\* =  $P < 0.01$ , \* =  $P < 0.05$ , ns = not significantly different.

	1	2	3	Total	G-value
Number of corollas visited					
A.					
20% sucrose (days 1–3)	162	35	7	204	—
40% sucrose (day 4)	48	1	0	49	13.79**
40% sucrose (day 5)	35	3	1	39	ns
40% sucrose (day 6)	47	19	1	67	ns
30% sucrose (days 1–3)	100	24	3	127	—
10% sucrose (day 4)	32	56	29	117	73.97**
Number of feeders visited					
B.					
20% sucrose (days 1–3)	176	26		202	—
40% sucrose (day 4)	47	1		48	4.62*
40% sucrose (day 5)	29	5		34	ns
40% sucrose (day 6)	40	13		53	ns
30% sucrose (days 1–3)	80	23		103	—
10% sucrose (day 4)	10	57		67	69.2**

ing energetic quality of nectars that we offered fit the general predictions of optimal foraging theory that as patch quality increases, search or travel time between patches decreases (Schoener 1971).

Little defense of feeders was observed throughout the study. During peak use periods (early morning or evenings) most feeders would simultaneously be occupied by several birds. Focal observations revealed that individuals were readily able to drink at a feeder upon arrival at the feeder site. Intrusion rates into the area were very high and only brief skirmishes were observed at feeders.

#### RESPONSES TO SUCROSE

Black-chinned Hummingbirds did not consume significantly different amounts of nectar when choices included 20%, 25%, and 30% solutions on each feeder. When the differences were increased to 10% and included choices between 20%, 30%, and 40% on each feeder, three repeated experiments showed no differences in the

amounts taken ( $\chi^2$ ,  $2 \times 3$ ,  $P > 0.05$ ). When the choices included a range of nectars of 10%, 20%, and 40% sucrose on each feeder, the hummingbirds showed a significant preference for higher sucrose concentrations taking almost four times as much 40% sucrose as either 10% or 20% sucrose ( $\chi^2 = 10.8$ ,  $P < 0.01$ ).

Calder (1979) suggested that during the dry season, hummingbirds may require more water than available in 20% nectar. To investigate the degree to which hummingbirds supplement nectar with water, on 12 May and 9 July 1987, (air temperatures at 28°C and 33°C, relative humidity at 10% and 18%, respectively), water and 20% sucrose were offered at midday. Hummingbirds selected significantly more 20% sucrose ( $\bar{x} = 5.73$  g/tube, SE = 0.012) than pure water ( $\bar{x} = 0.137$  g/tube, SE = 0.015,  $t = 22.7$ ,  $n = 30$ ,  $P < 0.001$ ). Calder (1979) suggested that hummingbirds in warm environments (> 35°C) would require some supplementary drinking water to maintain osmotic homeostasis of body fluids. Although some water was taken, nectar remained the primary water source for hummingbirds in our study.

TABLE 2. Total net weight (g) of nectar removed by Black-chinned Hummingbirds from 10 feeders, each with three test nectars for six experiments (A-F). Abbreviations: SA = saccharin, SU = sucrose, EQ = Equal, AS = aspartame, CMC = carboxy methyl cellulose,  $\chi^2$  = Friedman's nonparametric analysis of variance chi square value,  $F$  = comparison of differences between nectars in ANOVA, \*\* =  $P < 0.01$ , ns = not significantly different. See text for methods of nectar preparation. Experiments B, C, and F have CMC in viscosity equal to 20% sucrose.

Experiment				$\chi^2$	$F$
A.	<u>20% SU</u> 2.63	<u>27.3% SU</u> 3.22	<u>0.045% SA</u> 0.43	14.0**	10.9**
B.	<u>20% SU</u> 5.80	<u>2.47% EQ</u> 0.88	<u>2.47% EQ + CMC</u> 0.89	15.0**	345**
C.	<u>20% SU</u> 5.84	<u>0.1% AS</u> 0.51	<u>0.1% AS + CMC</u> 0.59	15.8**	265**
D.	<u>20% SU</u> 1.21	<u>20% SU + 0.0225% SA</u> 1.51	<u>20% SU + 0.045% SA</u> 1.49	ns	ns
E.	<u>20% SU</u> 5.09	<u>20% SU + 2.43% EQ</u> 4.14	<u>20% SU + 4.87% EQ</u> 4.21	ns	ns
F.	<u>20% SU</u> 4.33	<u>40% SU</u> 4.28	<u>0.065% SA + CMC</u> 0.28	13.54**	27.59**

#### RESPONSES TO ARTIFICIAL SWEETENERS

Artificial sweeteners were ignored by the hummingbirds. Jackinovich (1981) observed that, in contrast to sugars, most of the nonsugar sweeteners are neither tasted uniformly by all mammalian species nor even preferred by many species. Insects do not prefer them nor are their sugar receptors usually stimulated by these compounds (Schoonhoven 1974). Thus, it appears that the Black-chinned Hummingbird may be included among those species which do not respond to artificial sweeteners. Twenty percent sucrose was preferred over equivalently sweet (to humans) saccharin, aspartame, and Equal (Table 2A, B, C). To determine if the artificial sweeteners were being avoided or rejected, they were added to nectars of 20% sucrose. In these cases no preferences were observed, indicating that the artificial sweeteners were ignored rather than rejected (Table 2D, E). Because the principal sweetener in Equal is aspartame, it was not tested alone with sucrose but was assumed to be nonaversive like saccharin.

#### EFFECTS OF VISCOSITY ON NECTAR SELECTION

Increasing the viscosity of artificial sweeteners with CMC did not enhance their acceptability (Table 2B, C, F). We also found that 20% sucrose

was preferred 14:1 in favor of 0.0478% CMC which was equal in viscosity to 20% sucrose (Friedman's ANOVA,  $\chi^2 = 14.8$ ,  $P < 0.001$ ). Tests with 5% sucrose plus a CMC solution equivalent in viscosity to 40% sucrose indicated that both 10% and 20% sucrose were preferred to this low sweet and high viscosity mixture (Table 3A). Thus, sweet (sucrose) stimuli rather than high viscosities are required to elicit feeding in Black-chinned Hummingbirds. To determine if increased viscosity could enhance consumption of adequately sweet nectars, 20% sucrose solutions with added CMC were tested. However, this increase in viscosity had no effect on nectar selection (Table 3B). A CMC solution with a 40% sucrose viscosity equivalence plus 15% sucrose was preferred over CMC alone but was equal in acceptance to 20% sucrose (Table 3C). While the 15% sucrose was sufficient to stimulate feeding, the greater viscosity from the added CMC did not cause increased consumption. These tests also indicated that CMC in test nectars did not inhibit consumption.

#### SUMMARY

Black-chinned Hummingbirds in our tests responded to sucrose concentrations as low as 10% but preferred 40% while the artificial sweeteners, aspartame, saccharin, and Equal, were ineffective stimuli. Plain viscous solutions, artificial

TABLE 3. Total net weight (g) of nectar removed by Black-chinned Hummingbirds from 10 feeders, each with three test nectars for three experiments (A-C). Abbreviations: SU = sucrose; 10 CMC = carboxy methyl cellulose solution with viscosity equal to 10% sucrose solution; 20 CMC = viscosity equal to 20% sucrose solution; 40 CMC = viscosity equal to 40% sucrose solution;  $\chi^2$  = Friedman's nonparametric analysis of variance chi square value; *F* = comparison of differences between nectar by ANOVA; \*\* = *P* < 0.01; ns = not significantly different.

Experiment				$\chi^2$	<i>F</i>
A.	<u>20% SU</u> 4.99	<u>10% SU</u> 2.87	<u>5% SU + 40 CMC</u> 0.65	13.6**	38**
B.	<u>20% SU</u> 4.40	<u>20% SU + 10 CMC</u> 5.87	<u>20% SU + 20 CMC</u> 2.91	ns	ns
C.	<u>20% SU</u> 5.40	<u>15% SU + 40 CMC</u> 4.84	<u>40 CMC</u> 0.43	46.6**	186**

sweeteners with CMC, and viscous solutions with inadequate sucrose concentrations all proved to be nonstimulatory. Increasing the viscosity of sucrose solutions did not elicit increased consumption. There was no evidence that artificial sweeteners and CMC were aversive stimuli. In conclusion, we believe that chemosensory mechanisms rather than physical measures of viscosity are responsible for the sensory evaluation and the subsequent selection of sucrose nectars. Our results support the model presented by Kingsolver and Daniel (1983) which predicts that even with the added feeding costs associated with higher nectar viscosities, higher sucrose concentrations are preferred by hummingbirds.

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