

FIGURE 2. The 1973 breeding season. Top: as in figure 1; except that ordinate indicates the average number of blossoms per $2\text{ m} \times 2\text{ m}$ plot; arrows denote first appearances of respective flower types. Bottom: as in figure 1; except that no open bars (brooding activity of "late-nesters") are shown. Middle, left: census of forests; ordinate indicates the average number of female Broad-tailed Hummingbirds detected per census hour.

fitness of nesting females. An abrupt end to a nesting season, as happened in 1972, may exemplify the latter sort of difference.

This work was partially supported by a grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History and by Biomedical Sciences Support Grant FR 07002 from the General Research Support Branch, Division of Research Resources, Bureau of Health Manpower Education, National Institutes of Health. I extend sincere thanks

to Stephen Sponberg for many plant identifications, and especially to William A. Calder, H. Ronald Pulliam, Graham Pyke, and David Inouye for encouragement, criticism, and generous field assistance.

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 and Rocky Mountain Biological Laboratory, Crested Butte, Colorado 81224. Accepted for publication 28 August 1974.

DURATION OF FEEDING BOUTS AND RESPONSES TO SALT SOLUTIONS BY HUMMINGBIRDS AT ARTIFICIAL FEEDERS

D. M. BROOM

The feeding methods of hummingbirds depend upon the characteristics of the flowers from which they feed, nectar quantity and quality, crop volume, and rate of absorption from the gut (Skutch 1952, Grant and Grant 1968, Hainsworth and Wolf 1972, Snow and Snow 1972, Wolf et al. 1972, Hainsworth 1973). In this paper, I report on interspecific differences in feeding bout duration in seven species of hummingbirds. Most observations were made at artificial feeders, but a few birds were observed feeding from

flowers. Certain other aspects of feeding behavior are described (see also Broom 1975).

Two of my experiments were prompted by Bacon's (1973) observation of a hummingbird hovering over the sea and apparently drinking. The hummingbird may have been responding to its reflection or drinking to obtain water or salt. I therefore tested the preferences of hummingbirds for salt solutions of different concentrations in artificial feeders.

Hummingbirds of 10 species were observed feeding from 15 artificial feeders at a home in Aripo Valley, Trinidad, between October and December 1972. A few birds of three species feeding from hibiscus flowers were observed with binoculars from a distance of 20 m. The duration of each feeding bout, i.e. the time that the bill tip was inside the flower, was recorded. In Experiment 1 bouts were timed with a stopwatch from distances of 4 to 10 m. In Experiments 2 and 3, hummingbird consumption of liquid

TABLE 1. Duration of feeding bouts of three species of hummingbirds at hibiscus flowers.

Species	N	Mean duration of drinks (sec)	Comparison ^a of species 1 with:	
			species 2	species 3
1. <i>Amazilia tobaci</i>	21	2.4 ± 1.8	$P < 0.001$	$P < 0.001$
2. <i>Chlorestes notatus</i>	13	1.0 ± 0.5	-	$P < 0.001$
3. <i>Phaethornis longuemareus</i>	45	< 0.5	$P < 0.001$	-

^a 2-tailed Mann-Whitney U tests (Mann and Whitney 1947).

from four feeders on two posts was measured. The frequency and duration of visits by hummingbirds seemed unaffected by the presence of an observer 4 m away.

Prior to all observations and during Experiment 1, the feeders contained 0.55 molar sugar solution and red food coloring. Feeding bouts consisted of series of drinks with pauses when a bird hovered in front of the feeder before returning to drink again. When a bird was absent from the feeder for more than 2 sec, the total time spent drinking, excluding pauses, was recorded as a feeding bout. If one bird was displaced by another, or if it returned to a feeder within one min, the record was ignored. Approximately 20 hummingbirds were observed.

In Experiment 2 the four feeders contained either distilled water or colorless salt solution (0.1 or 0.5 M NaCl). In Experiment 3 the feeders contained either red-colored sugar solution (0.27 M) or this same sugar solution with salt added to strengths of 0.03, 0.05, 0.07, 0.125, 0.25 or 0.31 molar NaCl. Hummingbirds feeding on the normal sugar solution showed no preference for upper or lower feeders but did prefer feeders on one post to those on the other. Therefore, in Experiments 2 and 3 one type of solution was put in the upper left (A) and lower right (D) feeders and the other in the lower left (B) and upper right (C) feeders. The amount of each solution drunk by hummingbirds was recorded by measuring the levels in the feeders initially and after 20 or 30 min. After each choice test, the four feeders were filled with the normal sugar solution for at least 30 min before the next test was started.

FEEDING FROM FLOWERS

Hummingbirds of three species were observed feeding from hibiscus flowers. The duration of bouts (table 1) was greatest for Copper-rumped Hummingbirds (*Amazilia tobaci*) and least for Little Hermits (*Phaethornis longuemareus*), who drank too briefly to be timed accurately.

EXPERIMENT 1

Seven species of hummingbird fed on sugar solution in the feeders sufficiently frequently to allow comparison among species (table 2). Feeding bouts of the Little Hermit were significantly briefer than those of the six other species; feeding bouts of the White-chested Emerald (*Amazilia chionopectus*) were significantly briefer than those of the remaining

TABLE 2. Duration of feeding bouts of seven species of hummingbird at artificial feeders.

Species	N	Mean duration of bout (sec)	Comparison ^a with	
			<i>P. longuemareus</i>	<i>A. chionopectus</i>
<i>Glaucis hirsuta</i>	18	8.8 ± 4.4	$P < 0.01$	$P < 0.05$
<i>Phaethornis longuemareus</i>	5	3.2 ± 1.4	-	$P < 0.01$
<i>Florisuga mellivora</i>	28	8.9 ± 5.2	$P < 0.01$	$P < 0.05$
<i>Anthracothorax nigricollis</i>	16	8.3 ± 2.3	$P < 0.01$	$P < 0.01$
<i>Chlorestes notatus</i>	7	8.9 ± 3.4	$P < 0.01$	$P < 0.05$
<i>Amazilia chionopectus</i>	32	6.7 ± 2.5	$P < 0.01$	-
<i>Amazilia tobaci</i>	11	8.8 ± 3.1	$P < 0.01$	$P < 0.05$

^a 2-tailed Mann-Whitney U tests (Mann and Whitney 1947).

five species. Differences among other species were not statistically significant.

Other differences in feeding habit among species of hummingbirds were noticed. Little Hermits, Rufous-breasted Hermits (*Glaucis hirsuta*) and Green Hermits (*Phaethornis guy*) flew close to the ground and fed from the lower feeders. The drinks which made up each feeding bout were briefer, especially for the Little Hermit, than for other hummingbirds. Between bouts, several White-chested Emeralds perched within 2 m of a feeder and attempted to drive off other hummingbirds which approached. Black-throated Mangoes (*Anthracothorax nigricollis*) seemed the most successful at driving off other species, and Hermits were most easily displaced, but this was not studied systematically. Throughout most of the observation periods a Brown Violet-ear (*Colibri delphinae*) was present, but it rarely visited the feeders. It often flew out and caught insects on the wing.

EXPERIMENT 2

When the normal sugar solution was replaced by colorless distilled water or salt solution, most hummingbirds drank for less than 0.5 sec. The number of visits to the feeders declined rapidly (fig. 1), and very little of either solution was taken. Visits to water or salt solution were similar in number, but those to the salt solution were slightly longer (table 3). Twenty-four percent of the visits to the 0.5 M solution lasted for more than 0.5 sec, but only 9% of those to water lasted this long ($P < 0.1$, 2-tailed binomial t-test).

EXPERIMENT 3

In three control experiments lasting a total of 60 min, in which all four feeders contained sugar solution, the amount taken from feeders A and D was almost equal to that taken from feeders B and C (fig. 2). When two of the feeders contained salt at a concentration 0.07 M or less, the salt plus sugar solution was taken in proportions equal to the plain sugar solution. When the concentration was 0.125 M or

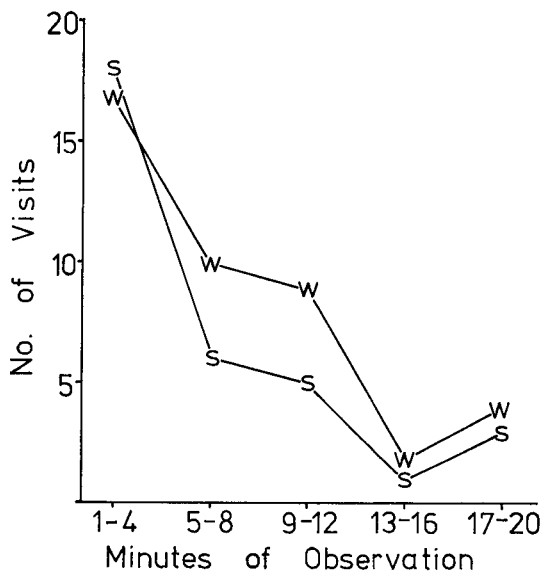


FIGURE 1. Decline in number of visits by hummingbirds of seven species to water (W) and 0.5 molar salt solution (S) in feeders during a 20 min. observation period.

greater, only 20% of the total amount drunk was salt and sugar mixture. In the control experiments 1.8–3 ml/feeder/min were taken, whereas in feeders with a salt concentration of 0.125 molar or higher, it was always less than 1.0 ml/feeder/min. Some of these salt-sugar mixtures were taken when first presented. Later in the experiment, the hummingbirds moved to other feeders after a brief taste, so a longer experiment might show more obvious avoidance of salt.

DISCUSSION AND CONCLUSIONS

Hummingbird species differ consistently in the duration of feeding bouts at artificial feeders. The Little Hermit had the briefest feeding bouts at artificial feeders and hibiscus flowers. Snow and Snow (1972) also observed a short drink. The White-chested Emeralds, which sat near the feeders, had shorter feeding bouts than the other species which sat further away. Two of these other species were fairly small, and three were fairly large, but they varied little in feeding bout duration. Larger species have larger crops (Hainsworth and Wolf 1972), but, due to differences in the rate of liquid uptake (Hainsworth 1973), two species which differ in size may fill their crops in feeding bouts of similar duration.

That hummingbirds drank much less sugar solution

TABLE 3. Duration of visits by hummingbirds of seven species^a to water and salt solutions.

Water		Salt solution	
No. visits <0.5 sec	Total no. visits	No. visits <0.5 sec	Total no. visits
5	34	0.1M:7	33
6	67	0.5M:13	54

^a Species listed in Table 2.

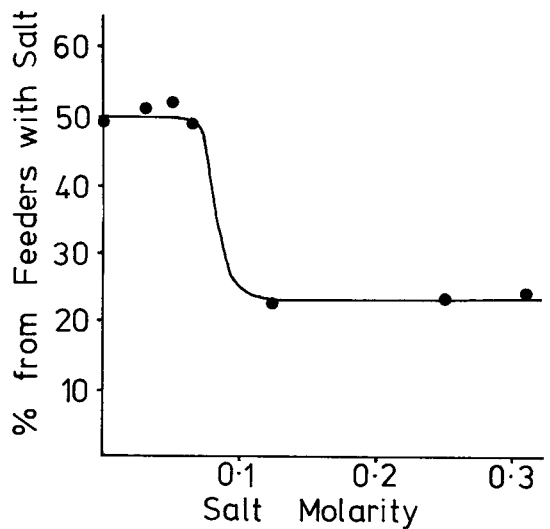


FIGURE 2. The percentage of the total amount drunk by hummingbirds of seven species (listed in table 2) from four feeders, containing sugar solution only or sugar solution plus salt at one of six concentrations.

if it included high concentrations of salt is not surprising, but it is of interest that the concentration at which some avoidance was first evident was 0.07–0.125 molar. The concentration which first reduces hummingbird intake is considerably weaker than that of sea water (0.5 M). Little of the water or salt solution with no sugar was taken, but more visits longer than 0.5 sec were made to the salt solution. Thus it seems possible that the hummingbird observed by Bacon (1973) may have drunk small amounts of sea water for the salt.

I am grateful to Peter Rapsey for allowing me to conduct these experiments at the hummingbird feeders at his house. I also thank my wife, Sally Broom, for help with observations and P. R. Bacon for his comments on the manuscript. This work was conducted while I was a Visiting Lecturer at the University of the West Indies, St. Augustine, Trinidad.

LITERATURE CITED

- BACON, P. R. 1973. Hummingbird drinking seawater. *Auk* 90:917.
- BROOM, D. M. 1975. Feeding methods of some Trinidad hummingbirds. *J. Trinidad Field Nat. Club* 1975:11–16.
- GRANT, K. A., AND V. GRANT. 1968. Hummingbirds and their flowers. Columbia Univ. Press, New York.
- HAINSWORTH, F. R. 1973. On the tongue of a hummingbird: its role in the rate and energetics of feeding. *Comp. Biochem. Physiol.* 46A:65–78.
- HAINSWORTH, F. R., AND L. L. WOLF. 1972. Crop volume, nectar concentration and hummingbird energetics. *Comp. Biochem. Physiol.* 42A:359–366.
- MANN, H. B., AND D. R. WHITNEY. 1947. On a test of whether one of two random variables is stochastically larger than the other. *Ann. Math. Stat.* 18:50–60.
- SKUTCH, A. F. 1952. Scarlet passion flower. *Nature Mag.* 45:523–525, 550.

- SNOW, B. K., AND D. W. SNOW. 1972. Feeding niches of hummingbirds in a Trinidad valley. *J. Anim. Ecol.* 41:471-485.
- 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.

Department of Zoology, University of Reading, Reading, England. Accepted for publication 27 May 1975.

ENVIRONMENTAL FAMILIARITY AND ACTIVITY: ASPECTS OF PREY SELECTION FOR A FERRUGINOUS HAWK

RON L. SNYDER
WILLIAM JENSON
AND
CARL D. CHENEY

Prey animal activity was first suggested as a major factor in prey selection by Cushing (1939) and by Ingles (1940). Metzgar (1967) showed that Screech Owls (*Otus asio*) capture more transient than resident mice (*Peromyscus leucopus*) and suggested that this preference was due to differential activity levels of the prey. Kaufman (1974) reported that Barn Owls (*Tyto alba*) selected more live (and therefore presumably more mobile) mice (*Mus musculus*) than dead ones, when offered a choice in a field enclosure. Snyder (1975) in a laboratory setting showed that a Red-tailed Hawk (*Buteo jamaicensis*) also selected the more active of two prey animals. The present paper reports selection preferences by a Ferruginous Hawk (*Buteo regalis*) offered a choice between two mice (*Mus musculus*) on each of 60 trials. Each trial consisted of presenting pairs of mice selected so as to include 6 combinations of 4 experimental treatment groups. The treatments manipulated the mice's familiarity with their environment and also their activity levels. The purpose of this experiment was to determine the effects of these manipulations on the hawk's choices and if the two treatments could be isolated as predation parameters.

One three-year-old, hand-reared, female Ferruginous Hawk was used. Its weight remained at 1650 g (± 30 g) throughout. The experiment was conducted in an outdoor enclosure measuring 10 \times 10 \times 3 m. The hawk was retained between trials on a perch in a wire mesh cage, attached to the roof of the east end of the enclosure. A remotely operated door allowed the hawk to leave this cage during selection trials and fly to either of 2 open-topped prey pens. These pens measured 2.6 \times 1.3 \times 0.6 m and were placed in opposite corners of the west end of the enclosure. Plexiglass was used in the ends of the prey pens facing the hawk to facilitate observation of the prey. Albino mice were divided into 4 treatment groups of 30 mice each for paired presentations, one in each prey pen. Two trials per day were conducted, one 4 hr after sunrise, and the second 3 hr before sunset. The 4 mouse treatment groups were: (1) "pen familiar" (F), (2) "pen unfamiliar" (U), (3) "drugged familiar" (DF), and (4) "drugged unfamiliar" (DU). All F group mice were allowed to move freely within a pen for 1 hr before the trial. The hawk's view of the pens was obscured by a drape during this familiarity time. The U mice were given no pre-trial pen exploration time. DF and DU mice were injected

intraperitoneally with 0.05 mg/kg Stelazine (Trifluoperazine HCl, a tranquilizer) 65 min before the trial in order to reduce their activity. Individual mice were randomly assigned to the left or right prey pens on each trial.

Each trial procedure was as follows: first, the door of the hawk cage was closed with the hawk inside and an opaque drape lowered. If a familiarity period was scheduled, the cover prevented the hawk's observing the mouse during this time. At the conclusion of the 1-hr mouse familiarity period, the appropriate mouse was placed in the other pen, the cage cover removed and the hawk allowed to observe both pens for 5 min. The door of the hawk cage was then opened and the hawk allowed to capture and consume one mouse. After capture the experimenter entered the enclosure and removed the other mouse, which was not used again. The data included the hawk's choice, and the latency to strike, measured from the opening of the cage to contact between the hawk and mouse.

To determine if there were in fact activity differences among prey groups, ten additional pairs of mice were prepared in the same manner as in the selection trials, and their activity was monitored during a 5-min period. Activity was measured by an observer recording the number of 25-cm² blocks on the floor of the prey pens that each mouse entered. This procedure provided a measure of mouse mobility comparable to the periods in which the hawk observed both mice in the main experiment. The hawk was not allowed to select the mice in this experiment.

The preference percentages in the table were analyzed in terms of the significance of a preferred proportion (Bruning and Kintz 1968). The unfamiliar mice were selected more often than familiar whether these familiar animals were tranquilized or not. Unfamiliar mice were also preferred over tranquilized-unfamiliar mice. When the choice was between two tranquilized mice, the hawk selected the unfamiliar; when between two familiar mice, the choices were equally divided. Latencies illustrated adaptation to the situation with a mean latency of 135 sec for the first 20 trials, 80 sec for the second 20, and 7 sec for the final 20. Side preferences were 34 left and 26

TABLE 1. Preference percentages for each of 6 pairings of the 4 mouse treatment groups with 10 trials per pairing.

Pairing	Condition and Hawk's preference percentages		Probability*
	Familiar	Unfamiliar	
1	F—20%	U—80%	<0.05
2	DF—10%	DU—90%	<0.05
3	DF—50%	F—50%	**
4	DU—0%	U—100%	<0.05
5	DU—30%	F—70%	**
6	DF—10%	U—90%	<0.05

* Probability determined by a sign test for the significance of a proportion (Bruning and Kintz, 1968).

** Not significant.