HUMMINGBIRD FORAGING BEHAVIOR AT *MALVAVISCUS ARBOREUS* VAR. *DRUMMONDII*

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ABSTRACT.—Changes in the appearance of *Malvaviscus arboreus* flowers are associated with changes in nectar reward. Nectar volumes found in day-1 flowers were generally larger and less variable than volumes found in day-2 flowers. Observations of nonterritorial Ruby-throated and Black-chinned hummingbirds (*Archilochus colubris* and *A. alexandri*) showed that they distinguished between flowers and preferentially visited the more profitable day-1 flowers. When sucrose solution was added to all day-2 flowers in one *Malvaviscus* patch, the birds stopped discriminating between flowers the first morning of floral enrichment.

These results indicate that the birds can respond to fairly subtle visual cues when determining the appropriate flowers to visit. The ultimate factor in determining which flowers to continue visiting, however, is the nectar reward. The birds learned to respond differently to the same proximate cue when it was advantageous to do so. *Received 13 March 1980, accepted 22 April 1980.*

HUMMINGBIRD foraging behavior can be viewed as a series of hierarchial decisions made among available options (Hainsworth and Wolf 1979, Gass and Montgomerie in press). A bird decides what habitat to forage in, chooses patches within that habitat, and selects flowers within that patch. A decision made at one level may limit the options and utility of decisions made at other levels. Whether or not a bird makes a "wise" decision depends partly on its ability to detect differences in profitability (Gass and Montgomerie in press) and to act upon those differences.

This study examines the ability of hummingbirds to assess differences among *Malvaviscus arboreus* var. *drummondii* flowers of different profitability within a patch and to adjust their foraging behavior accordingly. Three specific questions were asked: How did nectar volumes available to birds vary with flower age? Did birds discriminate between flower ages and prefentially visit the more productive flowers? Could their foraging behavior be modified by adding sucrose solution to the less productive flowers?

METHODS

The study was conducted at the Brackenridge Field Laboratories of the University of Texas at Austin from the end of July through September 1979. *Malvaviscus arboreus* var. *drummondii* is abundant in this 32-ha research reserve and is one of the main food-plants for female and juvenile Ruby-throated and Black-chinned hummingbirds (*Archilochus colubris* and *A. alexandri*) that forage there. It is a shrub-like hummingbird-pollinated perennial found from central Texas eastward into Florida. The showy red flowers last 2 days and undergo distinct changes in appearance during this time. The first day a flower is open, the staminal column bearing anthers and stigma extends above the petals, the petals tightly overlap, anthers are yellow with fresh pollen, and the style branches are erect. By the second morning the petals have partially unfurled with their edges starting to curl. Anthers are no longer yellow, and style branches are starting to droop.

I measured nectar volumes in uncovered flowers to see if amounts of nectar available to birds in day-1 and day-2 flowers differed significantly. Every 2 h, starting at dawn, I removed nectar from 15 flowers of each age chosen randomly from one patch of *Malvaviscus*. All nectar was removed with a 10-μl capillary tube without destroying the flowers or reducing their future nectar production capacity.

I observed hummingbird visits to two patches of *Malvaviscus* used by nonterritorial hummingbirds to determine if birds preferentially visited day-1 flowers. Each time a bird visited a flower, I recorded the flower's age. All flowers were marked with small white tags numbered "1" or "2" so that visited flowers

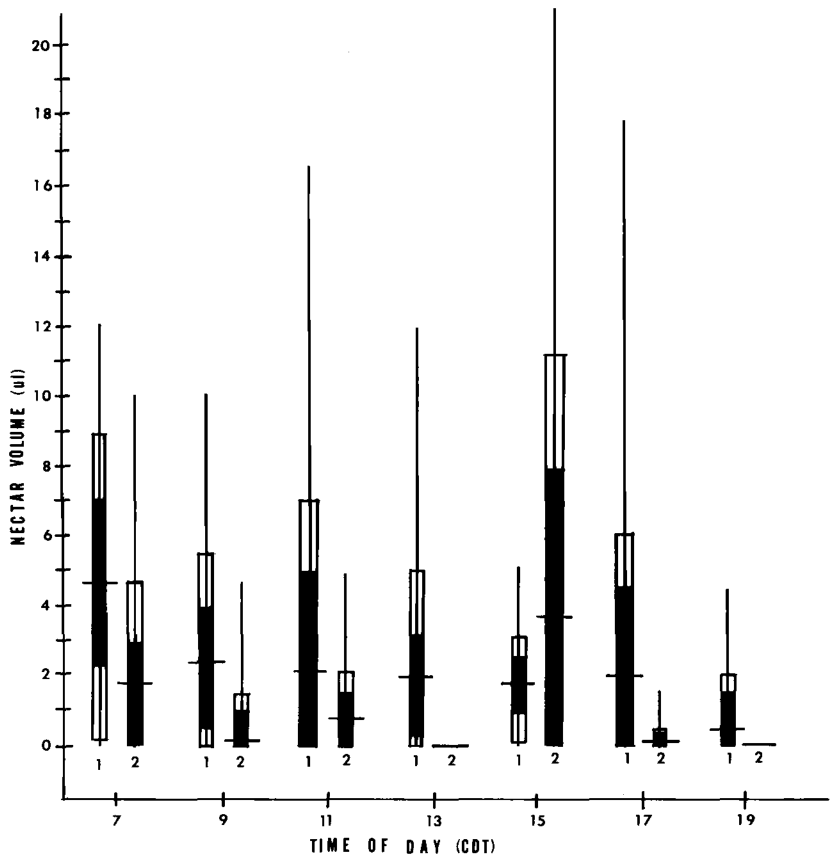

Fig. 1. Nectar volumes of day-1 and day-2 *Malvaviscus* flowers at different times of the day. Mean is indicated by horizontal bar, range by vertical bar, 1 SD on either side of the mean by open rectangle, and 95% confidence interval by black rectangle (after Gill and Wolf 1975).

could be accurately aged from a distance. I assumed that the tags appeared identical to the hummingbirds and would not be used by them as a cue to differentiate between flowers. At the beginning of each observation period all flowers in the patch were counted to determine the number of day-1 and day-2 flowers present. The relative availabilities of day-1 and day-2 flowers remained similiar during the July and September study periods (Table 1, $\chi^2 = 2.1$, $P > 0.30$). Observation periods started at dawn (ca. 0700) and continued for the next 4 h.

Day-2 flowers were artifically enriched at one of the patches to see whether the birds could recognize these new "good" flowers and include them in their foraging bouts. I added 20 μl of 30% by weight sucrose solution to all day-2 flowers at dawn and another 20 μl 2 h later. The amount and concentration of the added solution was equivalent to the average accumulated production in day-1 flowers (George 1980). Observations began immediately after the first sucrose addition at dawn and continued for the next 4 h. After 2 consecutive days of sucrose addition, solution was not added to day-2 flowers, and hummingbird foraging was observed for 4 h, beginning at dawn, to see whether the birds switched back to their previous foraging pattern.

Results

Nectar volumes obtained from day-1 flowers were generally larger and less variable than volumes found in day-2 flowers (Fig. 1). From 0700 to 1100, the average

TABLE 1. Number of hummingbird visits to day-1 and day-2 flowers. Significance of differences determined by a χ^2 test with 1 df.

Date	Number of flowers		Observed visits		χ^2	P
	day-1	day-2	day-1	day-2		
30 July	45	35	48	4	18.0	<0.001
31 July	37	40	55	9	20.5	<0.001
6 September	40	27	59	13	7.3	<0.01

volume in day-1 flowers was 3.0 μl. Nectar volumes in day-2 flowers averaged 0.9 μl in the morning, decreasing to almost zero in the afternoon, with the exception of the sample taken at 1500. Only three out of the 15 flowers sampled contained nectar, but those quantities were large (15, 20, 21 μl). These flowers probably had not been visited their first day, as day-2 flowers do not produce nectar (George 1980).

As day-1 flowers were energetically more rewarding than day-2 flowers and flower appearance changed with age, did birds discriminate between flower ages? If birds probed flowers without respect to their profitability, the expected number of visits to day-1 and day-2 flowers would be in direct proportion to that of the flowers occurring in the patch. Birds visited day-1 flowers, however, more often than expected (Table 1). While day-1 flowers comprised 56%, 48%, and 60% of the flowers in observed patches, they received 92%, 86%, and 87%, respectively, of the visits. The birds preferentially visited day-1 flowers, although they did not totally ignore day-2 flowers.

The birds stopped discriminating between flowers when sucrose solution was added to day-2 flowers (Table 2). By the 3rd h of observation on the first morning of floral enrichment, birds no longer preferentially visited day-1 flowers. The birds did not discriminate between day-1 and day-2 flowers at all during the second morning of enrichment. When the patch was left unaltered after 2 consecutive mornings of enrichment, the birds did not begin to discriminate again until after approximately 3 h of foraging (Table 3).

DISCUSSION

Changes in the appearance of *Malvaviscus* flowers are associated with changes in nectar rewards that hummingbirds can expect to receive. The birds took advan-

TABLE 2. Number of hummingbird visits to day-1 and enriched day-2 flowers on 2 consecutive days. Significance of differences determined by a χ^2 test with 1 df.

Date	Number of flowers		Observation hour	Observed visits		χ^2	P
	day-1	day-2		day-1	day-2		
7 September	34	40	1	36	17	5.2	<0.02
			2	62	23	11.0	<0.001
			3	46	30	2.6	>0.05
			4	43	49	0.003	>0.95
8 September	47	32	1	20	8	0.8	>0.25
			2	24	11	0.5	>0.25
			3	28	20	0.003	>0.95
			4	26	20	0.02	0.90

TABLE 3. Number of hummingbird visits to day-1 and day-2 flowers after 2 consecutive days of enriching day-2 flowers. Flowers were not enriched. Significance of differences determined by a χ^2 test with 1 df.

Date	Number of flowers day-1	Number of flowers day-2	Observation hour	Observed visits day-1	Observed visits day-2	χ^2	P
9 September	40	47	1	12	7	1.2	>0.25
			2	13	11	0.2	>0.50
			3	28	18	2.1	>0.10
			4	41	13	11.0	<0.001

tage of this change to increase the amount of nectar obtained per foraging bout by preferentially visiting the more energetically rewarding day-1 flowers.

That hummingbirds and other nectarivorous animals distinguish between flowers of different profitability has been observed several times (Gottsberger 1967, Jones and Buchman 1974, Gill and Wolf 1975, Heinrich 1975, Gass and Montgomerie in press). Because nectar is concealed in flowers, birds probably use visible changes in flowers as cues to flower contents. Most often the cue appears to be a change in flower color (Gottsberger 1971, Gill and Wolf 1975, Schemske pers. comm.), although other changes such as a hole left by a nectar thief (Gass and Montgomerie in press) or predictability of spatial position of unprofitable flowers (Colwell et al. 1973) can be used. My observations suggest that they can learn to use fairly subtle cues to determine the appropiate flowers to visit. I did not detect any color changes in the flowers, although that possibility cannot be excluded. The birds could have detected a change not apparent to me, as hummingbird vision is more sensitive to longer wavelengths than human vision (Stiles 1976) and is also sensitive to near U.V. (Goldsmith 1980).

The ultimate factor used to decide which flowers a bird should continue visiting is the amount of nectar a bird receives. The nectar addition experiment shows that birds can learn to respond differently to the same external cues if their view of the reward associated with that cue changes. The switch to visiting day-2 flowers happened fairly rapidly when the reward found in them changed from a highly variable one to a predictably large one. The birds also appeared to remember the change from morning to morning, as they never distinguished between day-1 and day-2 flowers the second morning of floral enrichment. Even when day-2 flowers were left unaltered, the birds continued to visit them the first 3 h of observation.

Several questions about hummingbird learning ability and its effect on foraging efficiency are raised by these observations. Birds were able to detect changes in reward, because they occasionally probed day-2 flowers under normal conditions. How did the costs of probing day-1 and day-2 flowers and the movement between flowers influence the frequency of day-2 probes given the expected rewards? Did the birds generalize what they had learned at the altered patch to other *Malvaviscus* patches, or were they able to distinguish the altered patch as unique and feed at day-2 flowers only at that patch? How did the size of the reward in the altered day-2 flowers affect the birds' behavior? What would be the minimum reward per flower and minimum number of enriched day-2 flowers needed to produce the switch in foraging described in this paper? Answers to these questions will provide insight into the foraging behavior of hummingbirds and the possible rules they use to make foraging decisions.

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