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TIME BUDGET AND FORAGING SITE PREFERENCE OF THE CINNAMON HUMMINGBIRD IN COSTA RICA

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Information on the apportionment of time for maintenance and breeding activities is important for understanding the evolution of avian reproductive and foraging behavior (e.g., Verner 1965, Stiles 1971, Verbeek 1972). Birds that maintain feeding territories exclusive of the breeding season (e.g., hummingbirds) often utilize resources relatively stable in time and space. Floral nectaries represent such resources and provide opportunities for prolonged observation of an individual bird's activities. This study describes the time budget and pattern of inflorescence utilization by the Cinnamon Hummingbird (*Amazilia rutila*) at a tropical flowering plant during the dry season in Costa Rica.

The plant serving as a nectar source in this study was *Combretum farinosum* (Combretaceae). *Combretum* grows as a bush or liana, and in the latter case may climb high into the canopy. Inflorescences contain many flowers arranged in rows and each flower passes through several age-dependent color forms. On first opening the flower is green, changing to orange the second day, and red by the third day. Flowers on an inflorescence are often totally synchronized in development, but if not, the changes occur in waves along the inflorescence, so some degree of color uniformity is always achieved. Nectar is produced primarily by the green, first-day flowers, with a lesser proportion from orange flowers of the second day (D. Inouye, pers. comm.). Red, third-day flowers produce little or no nectar and may remain on the inflorescences for several days.

The general study area was located on a wooded

tract near the field station at Santa Rosa National Park, Guanacaste, Costa Rica. Two specific sites were selected for observation. Site 1 consisted of three separate patches of *Combretum*—A, B, and C. All three patches were linearly ordered, with patch A 3 m E and patch C 15 m W of B. Patch A was an understorey bush, while patches B and C were lianas supported in the canopy by large trees. Patch B was divided into three subzones—B₁, B_m, and B_n; and C, into two—C₁ and C_n. Site 2 was located in a canopy-supported *Combretum* vine.

Each site was occupied and defended by a Cinnamon Hummingbird. There is no evident sexual dimorphism in this species so the sex of territorial birds was not determined. Zone B_n was periodically occupied by a migrant Northern Oriole (*Icterus galbula*) that exhibited interspecific feeding territoriality at the *Combretum* nectar source (Schemske, in press).

Observations were made on the mornings of 19 and 20 February at Site 1 and 16 and 21 February at Site 2. Morning and afternoon observations were made at Site 1 on 18 February. During each period the time allocated by each Cinnamon Hummingbird to perching, feeding, miscellaneous flying, chasing, and preening was recorded, as was the time each bird was out of my sight. Timing was done with two stop-watches and a tape recorder run concurrently with an electronic metronome. The frequency of feeding visits to inflorescences of different developmental stages (i.e., colors) was recorded at Site 1, patch B, for the Cinnamon Hummingbird on the morning of 23 February.

RESULTS AND DISCUSSION

The time budgets of each Cinnamon Hummingbird are given in table 1. The combined observation time for both sites was 26.7 hr. Although each of the two hummingbirds observed had favored perching sites, they would often move to different spots around the periphery of their territories and cause me to

TABLE 1. Time budgets of two Cinnamon Hummingbirds at *Combretum farinosum*.

Site	Date	Perching	OOS	Feeding	Preening	Chasing	Flight	Total
1	18 Feb.	397.8(70.0)	125.1(22.0)	40.5(7.1)	+	3.4(0.6)	1.5(0.3)	568.3
1	19 Feb.	216.2(70.1)	60.5(19.6)	28.4(9.2)	0.5(0.2)	2.0(0.6)	1.0(0.3)	308.6
1	20 Feb.	162.7(72.2)	27.7(12.3)	23.8(10.6)	8.4(3.7)	1.7(0.8)	1.0(0.4)	225.3
2	16 Feb.	217.9(79.8)	29.0(10.6)	23.5(8.6)	0.6(0.2)	1.3(0.5)	0.8(0.3)	273.1
2	21 Feb.	154.8(68.3)	33.4(14.7)	33.3(14.7)	2.0(0.9)	1.0(0.4)	2.2(1.0)	226.7
Total		1149.4(71.7)	275.7(17.2)	149.5(9.3)	11.5(0.7)	9.4(0.6)	6.5(0.4)	1602.0

First number is amount of time in minutes in each activity. Number in parentheses represents percent of observation time in each activity. OOS—Out of sight.

lose sight of them. The percent of time each bird was out of sight (OOS) is considerable but most of this time was probably spent perching. There were no additional nectar food sources near either site but some time out of sight was probably spent feeding.

The range of values for percent feeding time (table 1) is similar to those reported for the Anna's Hummingbird (*Calypte anna*) by Pearson (1954) and Stiles (1971), and the Purple-throated Carib (*Eulampis jugularis*) by Wolf and Hainsworth (1971). In these studies both hummingbird species spent a small proportion of their time catching insects, and Wolf (1970) observed much flycatching by several hummingbirds during the winter in Guanacaste Province. Although insects were abundant on the flowers of *Combretum*, no insect-catching by Cinnamon Hummingbirds was observed.

The variation in percent feeding time at each of the sites was not a function of the number of nectar-producing inflorescences available on any given date. If food resources are not limiting, feeding time may be a function of time spent in energetically expensive activities. At sea level and 20°C, the hovering-flight metabolic rate of a hummingbird the size of a Cinnamon (5 g) is approximately five times resting metabolic rate (Hainsworth and Wolf 1972). Hence, it is reasonable to hypothesize that increased accessory flight time (i.e., flight exclusive of feeding) will require additional feeding time to maintain energy balance. This trend is suggested here as the sum of flight and chasing time percentages of the Cinnamon Hummingbird for the five sampling dates and is positively correlated with percent feeding time ($r = 0.93$, $P < 0.05$).

The Cinnamon Hummingbird at Site 1 spent less than 33% of its feeding time at zone B_n during the presence of the territorial Northern Oriole, while more than 92% of its time was spent in this zone during oriole absence. The richness of patch B was demonstrated by the greater number of aggressive encounters directed at intruding hummingbirds by the Cinnamon Hummingbird. Of 135 total chases initiated by the Cinnamon Hummingbird, 115 occurred in patch B, 12 in patch C, and 8 in patch A. As all intruders at Site 1 were chased regardless of spatial position, these data provide an estimate of patch quality. Chases usually began before the invader had selected a specific feeding zone within a patch, thus more detailed estimates of invasion sites were impossible. The strong preference for zone B_n and, in general, patch B is explained by their high density of nectar-producing inflorescences. Of the 36 nectar inflorescences at Site 1, 27 were in patch B and 19 of these in zone B_n. Because of the paucity of nectar-producing inflorescences in patches A and C, and their distance from the favored perch at B₁, the time spent by the Cinnamon Hummingbird in these areas during absence of the Northern Oriole was minimized. When the oriole was present, these zones plus B_m and B₁ represented buffer feeding areas and may have permitted the continued existence of the Cinnamon Hummingbird at Site 1.

The distribution of feeding time and frequency of visits of the Cinnamon Hummingbird at patch B, Site 1, to inflorescences of different ages (table 2) was significantly different ($P < 0.01$) from that expected on the basis of the proportion of each inflorescence type available. The actual feeding time spent at each individual inflorescence was not obtainable, but the total time at each type divided by

TABLE 2. Feeding utilization of *Combretum farinosum* inflorescences by a Cinnamon Hummingbird.

	Inflorescence type				
	Green	Green and buds	Orange	Buds	Red
Number inflorescences visited	70	48	39	7	4
Total feeding time—seconds	488.5	199.0	181.0	14.0	1.2
Feeding time per visit—seconds	7.0	4.2	4.6	2.0	0.3

the total number of visits should give a reasonable estimate of inflorescence quality (i.e., nectar volume). It is apparent (table 2) that green inflorescences are the most productive as they elicit the greatest number and longest duration of visits. Although orange inflorescences provide less nectar per flower, they possess more flowers than a young inflorescence comprised of green flowers and buds. Hence, the feeding time per visit to an orange inflorescence is greater than that to a young green and bud type. Feeding visits to red inflorescences are rare and brief. It is not known if red flowers remain functional in pollination, but on the basis of visitation rate it appears that they would provide a trivial addition to seed set. This suggests that they may serve only as visual attractants or "flags" to hummingbirds.

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