

FEEDING ECOLOGY OF HUMMINGBIRDS IN THE HIGHLANDS OF THE CHISOS MOUNTAINS, TEXAS

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ABSTRACT.—The feeding habits of three species of hummingbirds were examined during the summer of 1975 in the highlands of the Chisos Mountains, Big Bend National Park, Texas. The Blue-throated Hummingbird (*Lampornis clemenciae*), the Broad-tailed Hummingbird (*Selasphorus platycercus*) and the Rufous Hummingbird (*S. rufus*) were common in the study area, the first occupying the mesic Cypress-Pine-Oak Association and the other two species inhabiting the Pinyon-Juniper-Oak Woodland.

Blue-throated Hummingbirds were almost exclusively insectivorous prior to the flowering of mountain sage (*Salvia reglia*), after which their diet began to include its nectar. Males fed outside their territories in the morning at nectar sources in the juniper woodland.

Selasphorus hummingbirds overlapped extensively in diet. *S. platycercus* was common prior to the full flowering of sage, and migrating *S. rufus* entered the area later, when the sage was in bloom. Males of both species typically established territories around large patches of the sage and open areas while females were relegated to smaller *Salvia* stands in the woodlands. Such a pattern is apparently maintained by the aggressiveness of the dominant males.

Recent examinations of tropical nectarivorous guilds (Feinsinger 1976, Feinsinger and Colwell 1978) have shown that such communities are organized about the distribution of nectar resources. Niche differences among tropical hummingbirds may result from aggression (Wolf 1970, Lyon 1976, Wolf et al. 1976), different foraging patterns (Linhart 1973, Feinsinger 1976), microhabitat selection (Stiles and Wolf 1970), or the exploitation of specific resources by highly specialized species (Snow and Snow 1972). Far fewer hummingbird species inhabit temperate areas than the tropics, and most species are migratory. North American hummingbirds differ from one another ecologically in the same ways as their tropical counterparts. These differences include habitat selection (Pitelka 1951, Lyon 1973, Yeaton and Laughrin 1976), spatial distribution of individuals through territoriality (Pitelka 1942, Cody 1968), and variations in foraging patterns (Feinsinger and Chaplin 1975, Yeaton and Laughrin 1976).

We examined the feeding ecology of three interacting hummingbird species with emphasis on their habitat partitioning and timing. We hypothesized that these characteristics would be important to the organization of a nectarivore guild where nectar

sources are uncommon. Such conditions appear to occur in the highlands of the Chisos Mountains during the summer.

STUDY AREA AND METHODS

Data were obtained in the Chisos Mountains (29°15', 103°18') of Big Bend National Park, Brewster Co., Texas during the summer of 1975. The study area was located in Boot Canyon (2,072 m) and centered in two highland plant associations: the Cypress-Pine-Oak Association and the Pinyon-Juniper-Oak Woodland (Wauer 1973). We also examined open areas located within Boot Canyon because they contained patches of nectar-producing flowers and were often visited by the hummingbirds.

The Cypress-Pine-Oak Association (henceforth "cypress woodland") occurs in the most mesic sections of the Chisos highlands, Pine and Boot canyons, where annual rainfall may exceed 500 mm (Wauer 1973). In the study area, this association occupies a narrow band along Boot Creek and is less diverse than the other woodland association. Arizona cypress (*Cupressus Arizona*), piñon pine (*Pinus cembroides*) and Graves oak (*Quercus gravesii*) predominate. The Pinyon-Juniper-Oak Woodland (henceforth "juniper woodland") is the most common plant association in the Chisos Mountains and in our study area. Typically, it contains piñon pine, emory oak (*Q. emoryi*), Graves oak and Mexican drooping juniper (*Juniperus flaccida*), which can be found on north-facing slopes from 1,650 m to 2,300 m. Within Boot Canyon, the juniper woodland adjoins the cypress woodland. Plant species diversity is greatest in the few open or exposed areas along upper Boot Creek, where herbaceous growth is abundant. Nectar sources were most plentiful in these areas.

TABLE 1. The relative abundance of nectar sources used by hummingbirds in the Chisos highlands.

Plant species	Relative abundance*	
	1 July	1 August
<i>Agave havardiana</i>	0.5	0
<i>Silene laciniata</i>	0	2.1
<i>Fouquieria splendens</i>	2.0	0
<i>Salvia regla</i>	8.1	85.3
<i>Castilleja elongata</i>	2.3	0
<i>Penstemon barbatus</i>	3.0	5.8
<i>Bouvardia ternifolia</i>	4.9	6.1

* Plants in flower per 100 m.

THE FLOWERS

All nectar sources visited by hummingbirds within Boot Canyon were recorded and their relative abundances were determined from transects through the two plant associations on 1 July and 1 August 1975 (Table 1).

Salvia regla (mountain sage), the most important plant resource for hummingbirds in the Chisos highlands, is common in open areas but unevenly distributed in the wooded areas. It is a multibranched shrub, usually pollinated by hummingbirds (Grant and Grant 1968). We recorded the availability of sage flowers bi-weekly along a 2.4-km transect in Boot Canyon (Fig. 1). Heavy flowering began in mid-July and continued through August, coincident with the onset of the mid-summer rains.

Two other plant species of local distribution were used to a lesser degree by hummingbirds in Boot Canyon: *Bouvardia ternifolia* and *Penstemon barbatus* (Correll and Johnston 1970). Both species occurred in rocky, primarily exposed, sites and characteristically flowered from June through August. These flowers most often were visited by nonterritorial hummingbirds as they rarely occurred in patches large enough to support territorial individuals.

Nectar volumes (in μ l) were measured with calibrated capillary tubes for 100 flowers of *S. regla*, *P. barbatus* and *B. ternifolia* at 07:00, prior to hummingbird visits. Nectar was most abundant at approximately this time, as hummingbird visits over the rest of the day reduced it to barely measurable levels. Quantities for each species were ($\bar{x} \pm SE$): *S. regla* = 4.26 ± 2.47 ; *P. barbatus* = 4.25 ± 1.83 ; *B. ternifolia* = 2.40 ± 1.85 . We counted the number of flowers per plant on 1 August (near peak flowering for all species). Values were ($\bar{x} \pm SE$): *P. barbatus* = 10.30 ± 5.53 ; *B. ternifolia* = 52 ± 10.4 ; *S. regla* = 6.4 ± 5.7 . Values for *S. regla* in open areas were significantly higher (25.3 ± 3.05 flowers/plant).

Insects and other small arthropods are important supplementary food for hummingbirds (Wagner 1946, Feinsinger 1976). A sampling of 150 corollas of *Salvia*, *Penstemon* and *Bouvardia* yielded no insects, suggesting that hummingbirds visited these flowers solely for their nectar. Comparable results were reported for bird-visited plants in Mexico (Wagner 1946). Numerous small insects were common in the foliage of plants in the cypress woodland. Surveys of these areas yielded beetles (Scolytidae), bugs (Psyllidae), thrips (Thripidae) and flies.

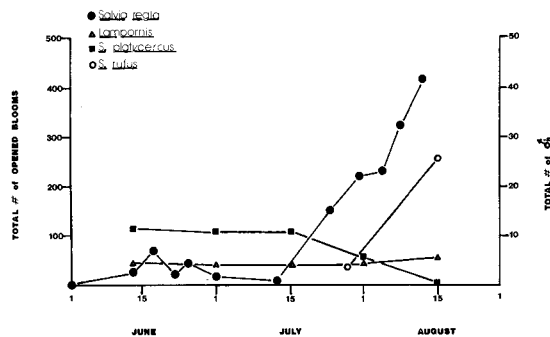


FIGURE 1. Hummingbird numbers in relation to available mountain sage (*Salvia regla*) along a 2.4-km transect in Boot Canyon (2,072 m). The left vertical axis indicates the total number of flowers opened. The right vertical axis represents the total number of male birds counted along the length of the transect.

THE HUMMINGBIRDS

We counted hummingbirds and noted their movements on 2.4-km transects taken through Boot Canyon. We also observed their foraging and territorial behavior around flowering patches of *Salvia*, *Penstemon*, and *Bouvardia*. We spent 18 h collecting data on individual transects through Boot Canyon. We conducted transects on the 1st and 15th of June, July and August, beginning at 07:30 and continuing for approximately three hours. The method consisted of walking along established trails at a steady pace and recording the sex and species of each individual seen or heard.

We watched hummingbirds at flowering clumps of sage for more than 400 h. A total of eight days (two days for 14 h; six days for 12 h) was spent in each of the two plant associations, with a specific patch of sage examined daily. The same procedure was used in studying the open areas and in examining the use of the other flowers by hummingbirds. At each observation site, the hummingbird species, sex, nectar extraction time, and total time at the plant were recorded.

The relative dominance of a hummingbird species is critical to its existence within a guild and may affect its patterns of use (Wolf 1970, Feinsinger 1976). Relative dominance was determined by noting the number of times a hummingbird succeeded in chasing an individual of a different species from the site. Individuals were not marked; however, most territories were so small that the resident male could be followed at all times. *Lampornis* individuals often left their territories on feeding forays. We noted the direction of flight and the timing of forays under such conditions.

RESULTS

Seven species of hummingbirds were recorded in the Chisos highlands during the summer of 1975. Only the Blue-throated Hummingbird (*Lampornis clemenciae*), Broad-tailed Hummingbird (*Selasphorus platycercus*) and the Rufous Hummingbird (*S. rufus*) occurred in sufficient numbers to be considered in this study. The Lucifer Hummingbird (*Calothorax lucifer*) was

TABLE 2. Mean number of observations/hour (instances of foraging or aggressive displays) of hummingbirds in three highland plant associations.

	<i>Lampornis</i> ♂ + ♀	<i>Selasphorus</i> (territorial)	<i>Selasphorus</i> (nonterritorial)
Cypress-Pine-Oak	4.00 ± .192*	.105 ± .067	.9 ± .067
Pinyon-Juniper-Oak	1.2 ± .159	.118 ± .096	4.3 ± .507
Open areas	.303 ± .015	17.6 ± 1.16	1.4 ± .042

* Mean values ± SE.

common in the Chisos lowlands in 1976 but we saw only five transients in the highlands during this study, all in early August. Rivoli's Hummingbird (*Eugenes fulgens*), White-eared Hummingbird (*Hylocharis leucotis*) and Costa's Hummingbird (*Calypte costae*) were each recorded once during the second week of August 1975.

BLUE-THROATED HUMMINGBIRD

This was the most abundant species of hummingbird in the cypress woodland of our study area (Table 2). No other hummingbirds established territories totally within this habitat; however, the territories of some male Broad-tailed Hummingbirds (primarily in the juniper woodland) did include portions of this association in segments along Boot Creek.

We observed three male Blue-throated Hummingbirds from June through mid-August 1975 on territories. Because of its large body size (7.90 g; Lasiewski and Lasiewski 1967), this species was dominant in conflicts, winning all interactions with both *Selasphorus* species ($n = 18$; $df = 1$; $\chi^2 = 9$; $P < 0.001$). Territories were elongate and parallel to Boot Creek. While on territories, males usually faced the creekbed which ran through the interior of the territory. This may be an efficient defense posture since most hummingbird intrusions occurred along the creekbed. The most common intruders of *Lampornis* territories were non-territorial transients, mostly female Broad-tailed Hummingbirds who used the creeks as flyways.

During the morning, *Lampornis* usually foraged outside of their territories in the surrounding juniper woodland (Fig. 2). These forays varied between two and twenty minutes. Approximately 16% of the day was spent on such forays. Prior to late June, nectar sources were rare in the Chisos highlands (Fig. 1), and those present were almost entirely in the juniper woodland and nearby open areas. The large size of Blue-throated Hummingbirds enabled them to be reasonably free from attack by the smaller hummingbirds. Most extra-territorially for-

aging *Lampornis* were recorded in the juniper woodland where there were few territorial hummingbirds and therefore few conflicts. Territorial males rarely foraged from 12:30 to 15:30; they resumed foraging at 15:30 and continued until dusk (20:30). Total foraging time in both morning and evening periods was similar (Fig. 2).

Male hummingbirds, when feeding in their territories in early June, ate only insects, gleaning them from vegetation as well as flycatching among swarming insects in the air above the creekbed. Wagner (1946) described similar feeding on insects by this species in Mexico. *Lampornis* occasionally fed at sage flowers after these opened in mid-July, but insects continued to dominate the diet within the territory throughout the summer. The moistness of the cypress woodland may account for the high relative abundance of insects in the territories of *Lampornis*.

BROAD-TAILED AND RUFOUS HUMMINGBIRDS

These two species occurred commonly in the juniper woodland and adjacent open areas (Table 2). Niche separation between them was largely temporal (Fig. 1). Broad-tailed Hummingbirds were present through July, after which large numbers of migrating Rufous Hummingbirds entered the Chisos highlands. Before the sage flowered, *S. platycercus* foraged at various plants, most of which are not hummingbird-pollinated (Table 1). Lyon (1973) reported similar behavior for this species in southeastern Arizona when hummingbird pollinated flowers were absent. At this time, *S. platycercus* territories were difficult to measure, and some males may have been non-territorial part of the time, perhaps acting as "facultative trapliners" (Feinsinger and Chaplin 1975). The dominant males stayed around copious sources of nectar, primarily *Agave*, in more open areas.

The *Selasphorus* hummingbirds overlapped in diet when both species occurred together briefly in the Chisos highlands (limiting similarity values = 0.77; overlap measure from Colwell and Futuyma 1971).

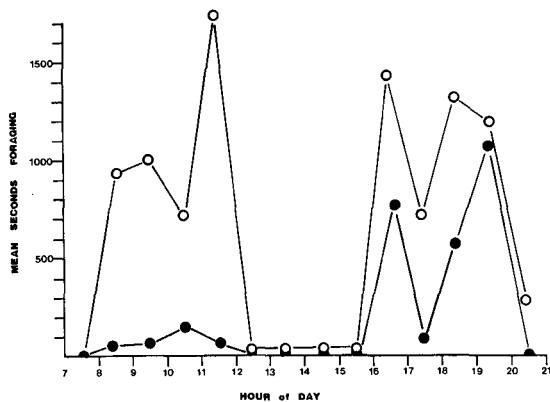


FIGURE 2. Active diurnal foraging periods of Blue-throated Hummingbirds in Boot Canyon. The mean number of seconds on foraging bouts (dark circles—within the territory; open circles—total foraging time) is represented on the vertical axis.

Lampornis, on its extra-territorial forays, foraged in a manner similar to both species of *Selasphorus* (similarity value for *S. platycercus* = 0.56; for *S. rufus* = 0.62).

Overall time budgets were similar for both *Selasphorus* species. Values for territorial males were: *S. platycercus* = 90.2% perching, 4.4% foraging; *S. rufus* = 88.6% perching, 5.5% foraging.

Much time was spent in territorial defense (5.3% of day for *S. platycercus*, 6.7% of day for *S. rufus*), due to high levels of aggression in early August when both species occurred together in the juniper woodland. In conflicts between the two species, *S. rufus* was slightly more successful; however, the difference was not significant ($n = 50$; $df = 1$; $\chi^2 = 3.48$; $P < 0.1$).

Selasphorus individuals in the juniper woodland selected different microhabitats. Males established territories in the open areas within and adjacent to the woodland where reduced vegetation probably allowed them maximum visibility for territorial defense. Nonterritorial birds were most common in the woodlands feeding on widely dispersed patches of sage (Table 2). Most territorial males avoided these woodland areas.

Territorial and nonterritorial *Selasphorus* fed upon sage at different times of day (Fig. 3). Nonterritorial birds fed earlier in the day ($r = -0.79$; $P < 0.001$; Fig. 3). Foraging of territory holders increased through the day ($r = 0.67$; $P < 0.01$; Fig. 3). Nonterritorial hummingbirds intruded into established territories during the morning presumably in order to forage on little-used sage. Aggressive displays by territory holders occurred more often (Fig. 4) at this time in

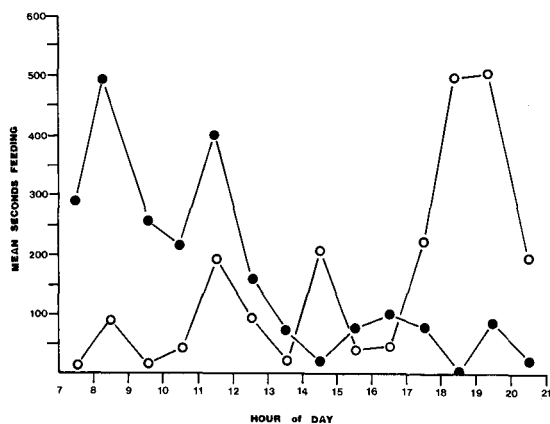


FIGURE 3. Use of sage by *Selasphorus* hummingbirds in the Chisos highlands. Nonterritorial birds (dark circles) fed primarily early in the day while territorial birds (open circles) foraged later.

response to these intruders. The number of territorial aggressive displays declined significantly during the day ($r = -0.77$; $P < 0.001$). Interestingly, nonterritorial individuals in the Pinyon-Juniper-Oak Woodland foraged significantly less as the day went on ($r = -0.91$; $P < 0.001$), even though they were increasingly free from conflicts with territorial males.

Nonterritorial *Selasphorus* (mostly females and immatures) foraged primarily on small patches of sage (also *P. barbatus* and *B. ternifolia*) in the juniper woodland, while territorial males controlled larger clumps of sage in the open areas along Boot Creek. During the morning when nectar was most abundant, nonterritorial individuals visited many clumps and often entered open areas. These intruders usually were chased from the area by territorial males. Such aggression relegated non-territorial birds to the woodlands and maintained habitat separation between territorial and non-territorial individuals. Territorial *Selasphorus* males rarely entered the woodlands. We suggest that this was due to the difficulty of defending such areas, and to the absence of sage patches large enough to support a territorial individual.

DISCUSSION

Blue-throated Hummingbirds were ecologically isolated from other hummingbirds occupying territories in the cypress woodland. Because of their size, they were efficient territory holders and were capable of using resources outside of defended areas. This pattern of extra-territorial feeding by *Lampornis* was documented by Lyon (1976).

Lampornis defended territories that usu-

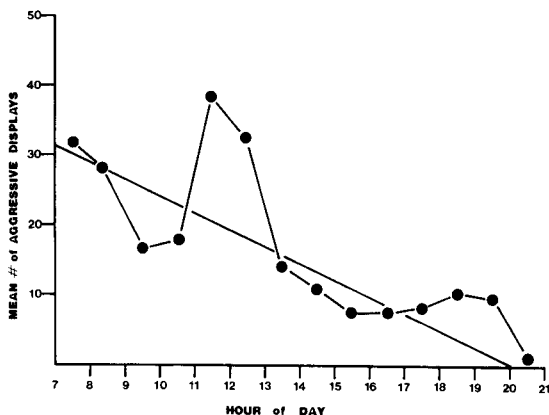


FIGURE 4. The timing of aggressive displays of two *Selasphorus* species (territorial males only).

ally were adjacent to streams. These mesic territories rarely were used for nectar, but served some function because they were vigorously defended even though vacated briefly while males foraged for nectar outside the defended areas (Fig. 2). There are three possible explanations for this pattern. First, insects were numerous in the cypress woodland probably more than elsewhere owing to the moisture provided by nearby streams. Blue-throated Hummingbirds are known to be wholly insectivorous during periods when flowers are unavailable (Wagner 1946). Few nectar sources were available in these areas before the sage bloomed. When these hummingbirds forage outside their territories, they may not be guaranteed a predictable nectar supply because of competition with other hummingbirds. A territory assures that insect resources exist in case food elsewhere is insufficient to meet daily energy demands. Most extra-territorial foraging bouts occurred in the morning (Fig. 2) when nectar was most plentiful, thus gaining a higher probability of finding unused supplies. Second, since the distances traversed between nectar sources can be important energetically (Wolf and Hainsworth 1971), *Lampornis* individuals may have maintained territories owing to their proximity to patches of flowers (Stiles and Wolf 1979). Third, while on territory male Blue-throated Hummingbirds called often throughout the day. Vocalization was common in June and began to decline in mid-July. Within the cypress woodland, the birds occurred in groups of three or four individuals. Aggressive interactions usually involved other conspecific individuals, probably within the same group. At a given vantage point three or four males could be heard vocalizing simultaneously. Territo-

ries within the cypress woodland may have been defended as individual breeding stations and these groups may have served as breeding leks for the purpose of attracting females (see Stiles and Wolf 1979).

The *Selasphorus* hummingbirds did not use the cypress woodland to any significant degree. Conflicts between them and Blue-throated Hummingbirds were infrequent. Even in the absence of the latter, the *Selasphorus* species probably would not use this habitat because it offers little nectar.

Feeding niches of the two species of *Selasphorus* overlapped significantly. The birds are nearly the same size and their time budgets and diets in the Chisos Mountains are similar. Competition from southbound Rufous Hummingbirds, whose arrival in the Chisos highlands coincides with peak flowering of sage (Fig. 1), apparently forced Broad-tailed Hummingbirds from their territories. Such effective dominance by Rufous Hummingbirds may have been because they outnumbered Broad-tailed Hummingbirds in early August (F. R. Hainsworth, pers. comm.). The former species is known to displace the latter as well as other congenics when in migration (Cody 1968, Kodric-Brown and Brown 1978).

The different diurnal patterns of foraging exhibited by territorial and non-territorial *Selasphorus* may have been the result of nectar availability. Fewer intrusions in the afternoon allowed territorial birds more time for foraging, dividing the time between territorial defense and foraging, a pattern previously reported by Stiles and Wolf (1970). This increased foraging time of territorial *Selasphorus* during the afternoon may also reflect a reduced nectar supply and a subsequent increase in the amount of time needed to collect a critical amount, since some thievery did occur.

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