

NECTAR AVAILABILITY AND HABITAT SELECTION BY HUMMINGBIRDS IN GUADALUPE CANYON

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ABSTRACT.—The importance of nectar availability and habitat selection to the seasonal occurrence, abundance, and nesting of Black-chinned (*Archilochus alexandri*), Broad-billed (*Cynanthus latirostris*), Violet-crowned (*Amazilia violiceps*), and Costa's (*Calypte costae*) hummingbirds was investigated. Periods of seasonal and daily nectar abundance were interspersed with periods of limited availability. Areas that contained greater quantities and more predictable nectar supplies tended to have more nests. Habitats selected for nesting differed among species, but were most alike for Black-chinned and Violet-crowned hummingbirds and for Broad-billed and Costa's hummingbirds. Results support the hypothesis that guilds are not always at resource-defined equilibrium. Hummingbird populations appeared to be above sustainable long-term levels in 1976, nearer such levels in 1977, and below these levels in 1980. Received 19 Sept. 1988, accepted 23 March 1989.

The relative importance of factors influencing the abundance of species and how shared resources are utilized have been the subject of numerous debates. Menge and Sutherland (1976), for example, have viewed predation, competition, and temporal heterogeneity as all being potentially important. Connell (1975, 1980) stressed that predation is frequently the major selective force organizing natural communities, while others such as Diamond (1978) have maintained that competition was perhaps more significant. In contrast, Wiens (1974, 1977, 1983) has proposed that many communities are often below saturation levels for the available resource, and thus competition is perhaps only important intermittently. Still others, such as Strong et al. (1979), have questioned whether observed community organization really differs from random assemblages (i.e., if patterns exist, are they the result of closely interwoven relationships between organisms, or do species occupy suitable available space without regard to the presence or absence of other species?).

Spatial and temporal heterogeneity, with respect to nectar availability and habitat selection, is examined in the present manuscript to determine the impact of these factors upon the seasonal occurrence, abundance, and nesting of each hummingbird species (see Baltosser 1986 for discussion of predation). Hummingbirds were selected for study because they depend on nectar sources that generally occur in discrete patches that are readily

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identified and quantified. They were also selected for study because of their small size and high mass-specific daily energy requirements, which make hummingbirds respond quickly to changes in their environment.

STUDY AREA

Guadalupe Canyon lies along the United States-Mexico border in extreme southwestern New Mexico and extreme southeastern Arizona. From its source in the Peloncillo Mountains of New Mexico, the canyon drains to the southwest, passing through Arizona before entering Mexico. Within Mexico the canyon joins the Río de San Bernardino, a tributary of the Río Yaqui. Data were generally collected from the 150-m-wide canyon bottom that rises from the International Boundary northeast into New Mexico, a distance of 8500 m (total area approximately 106 ha). Elevation of the canyon bottom ranges from 1305 m in the Arizona portion to 1366 m in the New Mexico segment. Guadalupe Canyon is surrounded by Chihuahuan Desert scrub vegetation that interdigitates with riparian vegetation in the creek bottom. On the basis of topography, exposure, and vegetation, I recognized three major habitats: riparian creek bottom, precipitous north-facing slopes, and xeric south-facing slopes. The creek bottom is characterized by numerous open areas interspersed with clumps of mature Arizona sycamores (*Platanus wrightii*) and Fremont cottonwoods (*Populus fremontii*), with understories of seepwillow (*Baccharis glutinosa*) and burro-brush (*Hymenoclea monogyra*) in central portions, and honey mesquite (*Prosopis glandulosa*), red barberry (*Berberis haematocarpa*), and netleaf hackberry (*Celtis reticulata*) near the edges. North-facing slopes rise abruptly from the canyon floor and are characterized by open areas interspersed with netleaf hackberry, one-seed juniper (*Juniperus monosperma*), oaks (*Quercus arizonica* and *Q. grisea*), soapberry (*Sapindus saponaria*), and agaves (*Agave schottii* and *A. parryi*), with dense shrub thickets composed of red barberry, honey mesquite, gray-thorn (*Condalia lycioides*), woolly buckthorn (*Bumelia lanuginosa*), and poison ivy (*Rhus radicans*). South-facing slopes rise gradually from the canyon bottom and are characterized by open areas with scattered agaves and ocotillo (*Fouquieria splendens*), or thickets of mixed species that include honey mesquite, little-leaf sumac (*Rhus microphylla*), and white-thorn (*Acacia constricta*).

METHODS

Local distribution of hummingbirds and the dispersion of resources were monitored biweekly from April through September using spot-map techniques (Williams 1936, Ken-deigh 1944). For the purpose of field surveys, Guadalupe Canyon was divided into 51 segments of equal size spaced linearly throughout the canyon. However, these segments were grouped into ten units for data analysis (Fig. 1).

Floral censuses designed to determine the phenology of nectar-producing plants and the relative abundance of nectar were conducted in 1976 and 1977 (Baltosser 1978). The phenology, location, and abundance (rare, common, abundant) of each species were measured every 7–10 days. Similar censuses, modified to obtain the actual number of flowers blooming, were conducted biweekly in 1980. Data for important species were obtained directly by counting the number of open flowers. When it was impractical to count all open flowers within a patch, flowers in smaller plots were counted and these data were used to extrapolate values for the entire patch. The above procedures were repeated in occasional cases in which the phenology of a species spanned more than one biweekly census.

Energy yields of important nectar-producing plants, based on the number of mg of sugar in each flower, were measured using methods of Roberts (1979) and Hainsworth and Wolf

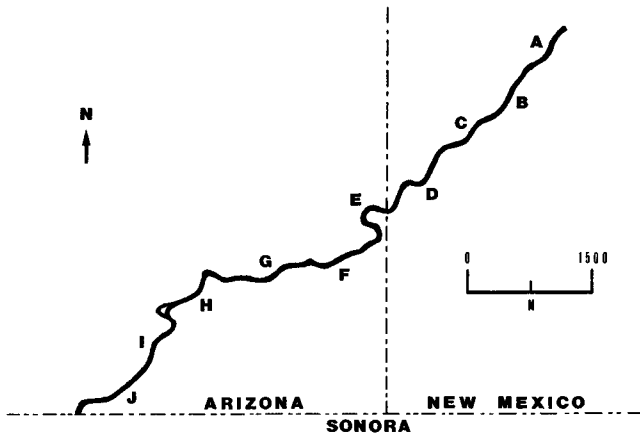


FIG. 1. Spot-map segments used for monitoring the local distribution of hummingbirds and resources in Guadalupe Canyon.

(1972). The amount of sugar per flower was measured using Roberts' method of spectrophotometric assays. Similar data were obtained using Hainsworth and Wolf's method by use of microcapillary tubes in conjunction with a pocket refractometer (see Bolten et al. 1979). The results obtained for each plant species using both methods were averaged and used in conjunction with those of floral censuses to measure biweekly standing crop nectar values, measured in joules, for each segment of the canyon.

Vegetation of nesting habitats was sampled in plots at randomly selected nests of each species. Selected nests were used as the center points of circular plots 30 m in diameter (707 m²). Within each plot, frequency, density, and cover values were measured for the following vegetation classes: height class III (trees > 3.5 m), height class II (trees and shrubs > 1 m ≤ 3.5 m), height class I (shrubs ≤ 1 m), and herbaceous plants.

Cover in each height class was estimated directly above and below a randomly selected point within each quarter of each nest plot. Density was estimated by counting all woody species occurring within the three height classes of each nest plot. Cover of small shrubs and herbaceous plants was estimated using a gridded 1-m² quadrat. When possible, height class II cover was measured by the same procedures. Cover of small trees and shrubs too tall for this method was projected onto the grid by a pole placed perpendicular to the grid. Cover produced by tall trees was estimated using two ocular tubes similar to the one described by James and Shugart (1970). Each tube provided a visual field of 1 m² at a known distance: 3.5 m for the shorter tube and 10 m for the longer tube.

Hummingbird nesting habitats were sampled from randomly selected nest plots of each species. Habitat descriptions and analyses were based on topography, dominant plant species, and 23 composite vegetation parameters (Baltosser 1978, 1983). Statistical analyses of these data included both univariate and multivariate vegetation analyses of the nest plots of each species. Univariate analyses (UNIVAR—D. M. Power, unpubl. data) of these parameters were used to test for differences between the habitats of the various hummingbirds. Multivariate discriminant function analyses (Dixon 1973) were then used to examine differences between the various habitats by considering intercorrelations between several variables, which resulted in reducing the number of significant variables from 14 in univariate analyses

to six. The discriminant analysis also computed a posterior probability for each nest plot that showed its chances of belonging to each bird species, i.e., just how similar each plot was to all others and how similar the nesting habitat of each hummingbird species (i.e., overall mean) was to other nesting hummingbird species.

Data on intra- and interspecific hummingbird interactions with respect to nectar availability were obtained from casual observations of encounters at floral resources, and from an experiment in 1980 designed to monitor the response and subsequent interactions of hummingbirds to reductions and spatial shifts in nectar supplies. Several hypotheses were established *a priori* to predict hummingbird behavior: (H_{O1}) hummingbirds will show no measurable response; (H_{A1}) hummingbirds will show measurable responses. Given that the former alternative hypothesis (H_{A1}) was accepted, then: (H_{O2}) each species will respond in the same manner; (H_{A2}) species will respond differently. Given that the former alternative hypothesis (H_{A2}) was accepted, then (H_{O3}) reductions in nectar supplies will have no effect on nesting success; (H_{A3}) nectar reductions will have an effect on nesting success.

Six Parry agave plants, all within 77 m of each other and the nests of three of the four hummingbird species present within Guadalupe Canyon at the time, were manipulated in the experiment. Additional agaves were present, but these were considerably farther from active hummingbird nests than were those chosen for study. I first observed hummingbird foraging behavior during selected periods for one day prior to each manipulation. At dusk of the control day, flowers that were open or ready to open were removed from all but one plant to ensure that flowers on only a single agave contained nectar the following day. The number of flowers removed and the number remaining were counted each time to calculate total energy values and the percent reduction. The same agaves were manipulated in the same manner during subsequent weeks; the only change was that the unmanipulated agave was arbitrarily changed. Hummingbirds quickly discovered, however, which agave contained nectar.

RESULTS

Hummingbirds. — The Guadalupe Canyon hummingbird guild consisted of four nesting species (all at the periphery of their breeding ranges), two transient species, and a single vagrant. Black-chinned (*Archilochus alexandri*), Broad-billed (*Cynanthus latirostris*), Violet-crowned (*Ama-zilia violiceps*), and Costa's (*Calypte costae*) hummingbirds all nested, whereas Broad-tailed (*Selasphorus platycercus*) and Rufous (*S. rufus*) hummingbirds were common seasonal transients. A single vagrant Lucifer Hummingbird (*Calothorax lucifer*) was observed only once.

The seasonal occurrence and abundance of hummingbirds in Guadalupe Canyon are shown in Table 1. Black-chinned and Broad-billed hummingbirds were present from April to September, while other guild members were present for shorter periods. The abundance of each species was similar among years, with the exception of the Black-chinned in 1980. The reduction in Black-chinned numbers in 1980 apparently resulted from an unusual and extreme freeze that occurred in December 1978. Foliage in segments A–E during 1980 was still, after nearly 17 months, reduced by 75%, based on gridded overlays of photographs from former years. Frost damage in lower segments (F–J) was not as extreme and vegetation had recovered to a greater extent by 1980.

TABLE 1
SEASONAL ABUNDANCE OF HUMMINGBIRDS IN GUADALUPE CANYON (NO. BIRDS/106-HA
STUDY AREA)

Species Year	Biweekly abundance										
	A	M	J	J	A	S					
Black-chinned											
1976	12	15	15	13	36	22	38	23	23	30	15
1977		12	16	18	26	21	26	21	25	15	12
1980		8	7	11	13	13	8	6	6	9	10
Broad-billed											
1976		3	3	3	9	9	14	14	15	17	5
1977		4	8	8	10	9	11	8	10	6	4
1980		5	5	6	6	7	5	6	6	4	6
Costa's											
1976				5	5						
1977			4	7	7	3					
1980			9	4							
Violet-crowned											
1976							3	7	7	13	7
1977					3	5	5	6	10	8	3
1980			1			4	6	8	6	10	4
Broad-tailed											
1976		15	20	20	1					8	10
1977		15	20	20						8	10
1980		10	10	5						5	5
Rufous											
1976							10	15	25	15	10
1977							10	15	25	15	10
1980							10	15	25	15	10
Lucifer											
1977				1							

The effects of the freeze were reflected in the distribution and number of Black-chinned nests during 1980. The number of Black-chinned nests in segments A–E in 1980 was only five, as compared to 21 and 17 in 1976 and 1977, respectively. Broad-billed and Violet-crowned hummingbird nest numbers during 1980 were not affected by the freeze. Presumably, this was because the Violet-crowned was never common in upper portions of the canyon (more affected segments), and plant species used for nesting by the Broad-billed were not damaged by the frost to the same degree as were the Arizona sycamores used for nesting by the Black-chinned.

The term "nesting season" as used in the present context refers to those months female hummingbirds were attending nests. The Black-chinned had the longest nesting season, followed in order by Broad-billed, Violet-crowned, and Costa's (Baltosser 1986). The first nesting period for the Black-chinned, which each year attempted to raise at least two broods, began in mid-April and terminated for many birds in mid- to late June. The second nesting period for the Black-chinned began in early July and extended into mid-August, although a few individuals were occasionally still feeding nestlings in early September.

Many Black-chinned females were engaged in feeding fledglings and in nest construction during the break between nesting periods. I observed four Black-chinned females constructing second nests in early July 1976 while still feeding large nestlings in their first nests. This did not, however, appear to be a universal trait. In 1977 only a single instance of overlapping nesting was observed for this species and no instances were recorded in 1980.

Broad-billed Hummingbirds nested during the same months as the Black-chinned and generally had two broods. In 1976 I observed a female of this species constructing a second nest near to her first, which still contained large nestlings. No other observations of overlapping nesting by this species were documented.

A single Violet-crowned Hummingbird occasionally arrived in Guadalupe Canyon in early May, but most did not occur until mid-June. Nesting for the Violet-crowned began the second week of July in 1976, in mid-June in 1977, and late June in 1980; each year nesting extended into September.

Costa's Hummingbirds have occurred in Guadalupe Canyon as early as March (Deuel and Parker 1972), but during my study they did not arrive until April. In 1976 and 1977 members of this species attempted to nest in May and early June, while in 1980 attempts were made only in May.

Availability of arthropods and nectar.—Foliage arthropods never appeared to be a limiting food supply, nor were they used to any extent. Even when there were "super abundant" numbers of planthoppers (Insecta: Homoptera) during 1980, hummingbirds did not alter their foraging to take advantage of this surplus. The only arthropods consistently consumed, other than those concealed in flower corollas, were flying Diptera and Ephemeroptera.

A tape-measure was used in 1980 to determine the biweekly availability of surface water throughout Guadalupe Canyon, because in 1976 and 1977 the occurrence of Ephemeroptera and Diptera appeared to be positively correlated with surface water availability. Precise measurements

of surface water were not made in 1976 and 1977, but its spatial-temporal occurrence was similar to that of 1980. Surface water was not abundant during late June, July, and early August 1980, and thus insects of both orders persisted only in segment C. Hummingbirds in this area continued to supplement their diet with these insects, but birds in other segments were not seen feeding on arthropods.

Nectar availability in Guadalupe Canyon exhibited two distinct seasonal peaks that were basically the same in 1976, 1977, and 1980 (Baltosser 1978, 1986). Each year the two flowering periods were separated by a conspicuous decline in nectar production in mid-June. Peak production of many plant species tended to be temporally distinct from peaks of other species, and each year was similar to the 1980 data shown in Table 2. As a result of temporally and spatially shifting nectar supplies, all hummingbirds were often forced to utilize the same plant species and many hummingbirds the same flower patches.

The first flowering period in 1976, 1977, and 1980 extended from late April through mid-June, with peak production between early and mid-May (Table 3, Baltosser 1978). During this period as many as 1005 kJ (standing crop) were available. Had this total been evenly distributed throughout the canyon, there would be approximately 100.5 kJ available in each 10.6-ha segment. However, as Table 3 shows, nectar supplies during this period were not evenly distributed, nor was nectar production equal among the 12 plant species in flower (Table 2). Hummingbirds foraged from all plant species in bloom during the first period, but 78% of the total energy was produced by *Penstemon pseudospectabilis* (Table 2).

The second flowering period in 1976, 1977, and 1980 extended from late June through early September, with peak production occurring from mid-July through early August (Table 3, Baltosser 1978). During this time as many as 747 kJ (standing crop) were available. If this were evenly distributed throughout the length of the canyon, there would be approximately 74.7 kJ available in each 10.6-ha segment. Nectar supplies during the second period were more evenly distributed than in the first (Table 3). The figure of 74.7 kJ is therefore a reasonably accurate assessment of nectar supplies in most segments during the second period. Thirteen plant species were in bloom and used by hummingbirds during the second flowering period, but 90% of the total production was by *Agave parryi* (Table 2).

Nectar requirements.—The relationship between available nectar and hummingbird abundance is shown in Table 4. Limited data from covered flowers of *Penstemon superbus*, *Penstemon pseudospectabilis*, *Anisacanthus thurberi*, *Agave parryi*, and *Epilobium canum* indicate that daily

TABLE 2
PHENOLOGY OF IMPORTANT NECTAR-PRODUCING PLANTS SHOWING THE BIWEEKLY CONTRIBUTION OF EACH SPECIES TO STANDING CROP
VALUES AND THE RELATIVE DISPERSION OF EACH THROUGHOUT GUADALUPE CANYON

Plant species	Flowering phenology (date and number of kl)												Segments present (%)
	Apr. 25	May 7	May 21	June 3	June 17	July 3	July 15	Aug. 2	Aug. 16	Sep. 2			
<i>Penstemon superbus</i>	18.11	14.96	6.04	1.75	0.37	0.03							55
<i>Cirsium neomexicanum</i>	5.66	38.67	34.58	9.66	5.16								92
<i>Penstemon pseudospectabilis</i>	137.51	546.85	306.74	62.61									4
<i>Castilleja</i> spp.	0.12	0.24	0.06	0.02	0.01			0.01				0.03	14
<i>Fouquieria splendens</i>	0.56	91.49	16.06										57
<i>Anisacanthus thurberi</i>	0.75	27.96	14.20	2.63									16
<i>Chilopsis linearis</i>		1.50	4.56	0.67									6
<i>Bouvardia glaberima</i>			0.32					0.04	0.21			0.09	8
<i>Agave schottii</i>				0.65	14.70	48.35	36.57	13.40	0.05				67
<i>Caesalpinia gilliesii</i>				3.72	5.51	2.39	0.11	0.03	0.16			0.05	8
<i>Penstemon barbatus</i>				0.08	0.51			0.01	0.03			0.52	14
<i>Erythrina flabelliformis</i>					1.22	0.93	0.21						18
<i>Agave parryi</i>						16.85	486.27	343.35	288.35			89.92	96
<i>Epilobium canum</i>							0.03	0.03	0.02				4
<i>Stachys coccinea</i>									0.01			0.03	8

TABLE 3
BIWEEKLY ENERGY (KJ) AVAILABILITY THROUGHOUT GUADALUPE CANYON DURING 1980

Date	Standing crop		Percent of total by segment									
	\bar{x}	SD	A	B	C	D	E	F	G	H	I	J
April 25	161	106	86	5	1	5	1			1		1
May 7	602	403	91	3	1	1	1	1	1			1
May 21	469	306	73	3	3	5	3	3	2	5	3	2
June 3	113	74	68	4	3	1	2	2	1	9	2	8
June 17	31	17	17	2	3	3	4	16	4	23	6	23
July 3	69	35	16	7	8	4	2	10	8	12	7	26
July 15	523	224	5	5	10	13	6	12	4	6	19	20
August 2	357	151	9	5	10	16	8	12	3	6	12	21
August 16	289	121	6	5	12	11	6	13	3	3	22	18
September 2	91	38	2	3	6	17	10	10	4	2	23	23

production varied, but was frequently four times that of standing crop values of flowers exposed to natural levels of exploitation. During each of the two flowering periods, minimum nectar requirements of hummingbirds in Guadalupe Canyon were on occasion met by available supplies (Table 4), but these data show that periods of seasonal abundance were interspersed with periods of limited availability.

The relationship between nectar supplies and their predictability of occurrence to nest dispersion and nesting success is shown in Table 5. A positive correlation between nectar abundance and the number of nests in each segment occurred during both nesting periods, but was statistically significant only during the second period ($r = 0.39$, $P < 0.19$ and $r = 0.87$, $P < 0.01$). An inverse correlation between the number of nests in each segment and nectar predictability (i.e., the greater the variability the fewer nests) occurred during the first nesting period but this difference was not statistically significant ($r = -0.49$, $P < 0.09$); there was virtually no relationship during the second period ($r = 0.01$, $P > 0.95$). Fledging success was not correlated with either amount of nectar or its predictability during the first period ($r = 0.23$, $P < 0.47$ and $r = -0.25$, $P < 0.45$, respectively), nor was there any correlation between fledging success and predictability during the second period ($r = -0.14$, $P > 0.68$). There was, however, significant correlation during the second nesting period between fledging success and the amount of nectar ($r = 0.61$, $P < 0.03$).

Nest sites.—Plant species used for nest sites by hummingbirds in Guadalupe Canyon are shown in Table 6. Black-chinned, Broad-billed, and to a certain extent Costa's hummingbirds utilized trees and shrubs in roughly the same proportions in which the various species occurred. In

TABLE 4
AVAILABLE NECTAR SUPPLIES AND HUMMINGBIRD NECTAR REQUIREMENTS

Date	Total available nectar ^a	Minimum nectar requirements ^b		
		1976	1977	1980
April 25	644	902	847	621
May 7	2408	1047	1290	811
May 21	1876	1114	1438	722
June 3	452	1319	1234	488
June 17	124	799	1073	695
July 3	276	1736	1438	863
July 15	2092	1651	1408	1054
August 2	1428	1931	2001	1219
August 16	1156	2413	1523	1321
September 2	364	1383	1031	993

^a Total available nectar = 4 × standing crop (kJ).

^b Minimum energy (kJ) required based on the number of birds present × 8.02 kJ/day for each 1 g body weight (Powers and Nagy 1988, Weathers and Stiles 1989); Black-chinned = 3.3 g, Broad-billed = 3.0 g, Violet-crowned = 5.7 g, Costa's = 3.0 g, Broad-tailed = 3.6 g, Rufous = 3.2 g, and Lucifer = 2.9 g.

contrast, Violet-crowned Hummingbirds selected plants for nest sites in a more specialized manner, selecting only one of the many available species.

Nest heights (m) of all hummingbird species, which included additional nests from other years (e.g., 1975 and 1978), were significantly different when compared using an analysis of variance ($F = 26.11$, $P < 0.01$). All species comparisons except Black-chinned vs Violet-crowned showed significant differences ($P < 0.05$). Broad-billed nest heights were extremely consistent, despite nests being in a variety of plant species. Mean, standard deviation, and sample size for each species are as follows: Black-chinned $\bar{x} = 5.8 \pm 2.8$ [SD], $N = 116$; Broad-billed $\bar{x} = 1.1 \pm 0.5$, $N = 33$; Violet-crowned $\bar{x} = 7.1 \pm 2.7$, $N = 14$; and Costa's $\bar{x} = 1.7 \pm 1.1$, $N = 11$.

Nest plot classifications based on the posterior probabilities calculated from six significant vegetation parameters (i.e., Height Class III Cover, Height Class II Cover, Height Class II Density, Height Class I Cover, Herbaceous Cover, and Foliage Height Diversity for Height Class III) of 46 plots resulted in 78% of the plots being grouped correctly. Mistakes in classification were made for all species, but seven of ten incorrectly classified plots were grouped incorrectly for the same reason. These seven plots were near margins of typical habitat for each species, and because of the large plot size (15-m radius), included portions of atypical habitat. The remaining three incorrectly grouped plots included two Broad-billed plots classified as Costa's and one Costa's classified as a Broad-billed.

TABLE 5
NEST DISPERSION AND NESTING SUCCESS IN RELATION TO NECTAR DISPERSION,
ABUNDANCE (STANDING CROP = KJ), AND PREDICTABILITY
(COEFFICIENT OF VARIATION)

Segment	1976-1977-1980 First nesting period				1976-1977-1980 Second nesting period			
	No. nests	No. successful nests	Standing crop	Coefficient of variation	No. nests	No. successful nests	Standing crop	Coefficient of variation
A	13	4	1846	1.00	5	3	135	0.75
B	5	0	75	0.78	5	2	95	0.89
C	6	2	43	1.03	7	7	192	0.94
D	9	5	66	1.16	8	1	251	0.96
E	3	2	42	1.08	0	0	127	0.89
F	3	0	45	0.99	5	4	235	0.87
G	4	1	29	1.14	2	2	73	0.82
H	4	1	69	1.11	7	4	114	0.83
I	7	3	30	1.64	13	4	333	0.97
J	19	7	54	0.48	23	9	397	0.81

Plant species found in Costa's plots, however, differed from those in Broad-billed plots by 72%, and thus even though both species had similar numerical values for many vegetation measurements, most were based on different species of plants.

Black-chinned Hummingbirds usually nested in relatively open areas interspersed with clumps of mature Arizona sycamore trees centrally located within the canyon, over or adjacent to the bare sandy bottom (Fig. 2). Most Black-chinned nests were in Arizona sycamores, 5-6 m above the bare creek bottom. As a result, many nests had relatively few small trees and shrubs immediately nearby. However, since plots had a radius of 15 m they occasionally included small trees and shrubs such as netleaf hackberry, one-seed juniper, seepwillow, and burro-brush near plot perimeters.

Violet-crowned Hummingbirds nested in areas with vegetation similar to that in Black-chinned plots. Instead of being centrally located within the riparian vegetation, Violet-crowned nests were at the edge of this vegetation in relatively open areas next to xeric hillsides (Fig. 2). Those portions of Violet-crowned plots nearest the creek bottom usually contained several Arizona sycamore trees underlain by seepwillow and burro-brush. Portions of Violet-crowned plots adjacent to open areas bordered by xeric hillsides had high densities of honey mesquite, red barberry,

TABLE 6
 PLANT SPECIES (NUMBERS PER HA⁻¹ ON NEST SITE PLOTS) AND THEIR USE AS NESTING
 SITES IN GUADALUPE CANYON BY THE VARIOUS HUMMINGBIRD SPECIES

Plant species	Black-chinned		Violet-crowned		Broad-billed		Costa's	
	Plant density	No. of nests	Plant density	No. of nests	Plant density	No. of nests	Plant density	No. of nests
<i>Platanus wrightii</i>	118	100	200	14	37		0	
<i>Celtis reticulata</i>	32	11	19		163	23	17	8
<i>Fraxinus velutina</i>	8	2	5		7		0	
<i>Quercus</i> spp.	8	2	2		40	3	— ^a	1
<i>Juniperus monosperma</i>	14	1	6		37		5	1
<i>Prunus persica</i>	— ^a	1	0		0		0	
<i>Berberis haematocarpa</i>	77		104		156	6	218	1
<i>Clematis ligusticifolia</i>	0		11		— ^a	1	0	
<i>Senecio salignus</i>	57		55		48	1	0	

^a Unsampled nest plots.

little-leaf sumac, gray-thorn, and large amounts of herbaceous cover composed primarily of grasses. All Violet-crowned nests were located in Arizona sycamore trees, their height above the ground averaging 7 m.

Broad-billed Hummingbirds nested in thickets near the edge of the canyon in areas primarily of northern exposure bordered by rock outcrops and typical Black-chinned habitat (Fig. 2). Dominant plant species within Broad-billed plots were small trees and shrubs, including netleaf hackberry, one-seed juniper, red barberry, honey mesquite, gray-thorn, little-leaf sumac, poison ivy, and woolly buckthorn. A few plots also contained small numbers of Arizona sycamore, Fremont cottonwood, and soapberry trees. Nests were in a variety of plant species, most were about 1 m above the ground, and many were within 1 m of rock outcrops.

Costa's Hummingbird nests were in the dry arroyo tributaries adjacent to the main canyon bottom or in areas of southern exposure (Fig. 2). The majority of plants within Costa's plots were xeric shrubs such as honey mesquite, little-leaf sumac, and white-thorn. Large trees were not present in plots of this species nor were many small ones. Nests tended, however, to be located 1–2 m above the ground in the few small trees (usually netleaf hackberry) that were present.

Foraging and experimental nectar reductions.—Virtually every hummingbird species in Guadalupe Canyon at one time or another was displaced from nectar sources by members of all other species. The trend, however, was for the larger Violet-crowned Hummingbird to be dominant, followed in order of decreasing dominance by Rufous, Broad-billed,

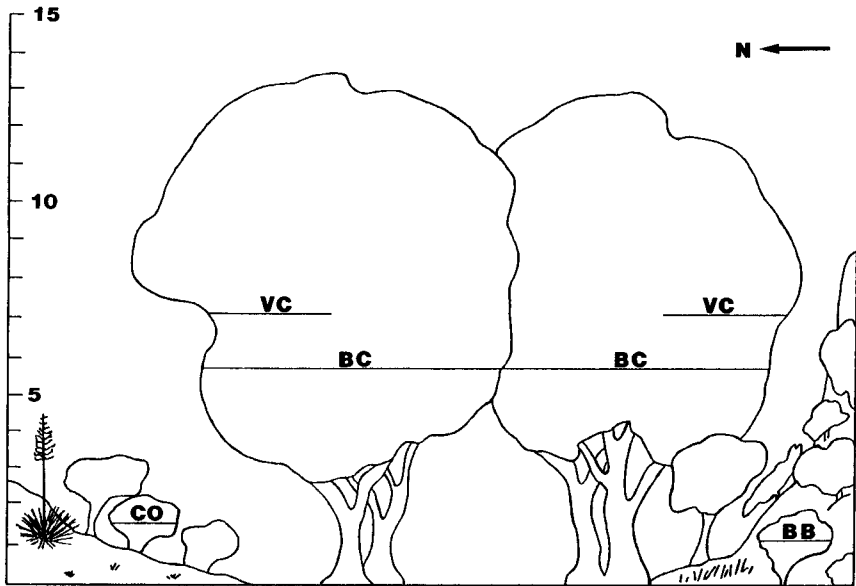


FIG. 2. Diagrammatic cross section of Guadalupe Canyon based on univariate and multivariate discriminant analyses showing the distributional patterns (horizontal axis), and mean nest heights (vertical axis) of Black-chinned (BC), Violet-crowned (VC), Broad-billed (BB), and Costa's (CO) hummingbirds.

Broad-tailed, Black-chinned, and Costa's hummingbirds. The data in Table 7 are based on only 12 hours of observation, but show typical interactions at unmanipulated agaves during the period of experimental nectar reductions.

The single greatest factor responsible for the disruption of female Black-chinned foraging was conspecific females. Rufous Hummingbirds were also a major source of disruption for Black-chinned and Broad-billed females. Interactions with Broad-billed and Violet-crowned hummingbirds also interfered with Black-chinned foraging. Rufous were interrupted in their foraging by conspecifics and by Violet-crowned and Broad-billed hummingbirds, although the latter were more frequently interrupted by Rufous Hummingbirds.

Sample size was insufficient for a statistical interpretation of the 1980 nectar reduction experiment because only three Black-chinned, two Broad-billed, one Violet-crowned, and five Rufous hummingbirds were present in the immediate vicinity of the experiment. Nevertheless, the amount of time (%) individuals spent feeding under natural and manipulated

TABLE 7
 INTERACTIONS BETWEEN HUMMINGBIRDS IN GUADALUPE CANYON WHILE FORAGING AT
AGAVE PARRYI PLANTS DURING JULY AND AUGUST 1980

Species displaced ^a	Species effecting displacement			
	B-C	B-B	R	V-C
B-C	10	3	7	3
B-B	0	0	5	1
R	0	3	4	4
V-C	2	0	2	1

^a Number of occasions a given species was displaced by another; abbreviations are as follows: B-C (Black-chinned), B-B (Broad-billed), R (Rufous), and V-C (Violet-crowned).

conditions was of interest. Standing crops of the six agaves within a 77 m radius (1.9 ha) of each other and single nests of Black-chinned, Broad-billed, and Violet-crowned hummingbirds were experimentally reduced on average (all plants combined) from 22.8 kJ to 7 kJ. Female Black-chinned Hummingbirds accounted for 38% of all foraging under natural conditions, but under conditions of reduced nectar supplies this dropped to only 5%. Male Black-chinned were not affected by reductions, nor were Rufous Hummingbirds of either sex or age in terms of the total proportion of time spent at flowers. In contrast, the Broad-billed increased its use of the single unmanipulated agave from 28% under natural conditions to 38%, while the Violet-crowned went from 9% to 28%, respectively. The increase in usage under experimental conditions by the Broad-billed and Violet-crowned is in part an artifact of sampling (i.e., decreased use by the Black-chinned), but each did in fact increase the length of time spent at the single unmanipulated agave under conditions of reduced nectar availability. Black-chinned and Violet-crowned hummingbirds nesting in the immediate vicinity (within 77 m) of nectar manipulations had complete nesting success. Broad-billed Hummingbirds, which generally succeeded in fledging young once they had hatched, lost one nestling early to predation and the other at a later date.

DISCUSSION

Breeding seasons and temporal occurrence. — The timing of avian breeding seasons has often been explained in terms of food availability, the eggs being laid during a period that anticipates the energetic costs of brooding and feeding young (Moreau 1950, Thomson 1950, Lack 1954, Perrins 1970, Immelmann 1971). Recent experimental studies by Ewald and Rohwer (1982), Davies and Lundberg (1985), Knight (1988), and Wimberger (1988) add support to this hypothesis. The nesting seasons of

hummingbirds in Guadalupe Canyon also seem to be related to the availability of food. Before mid-April and after mid-September there were very few nectar sources available to hummingbirds. Coincidentally, Black-chinned and Broad-billed hummingbirds nested only from mid-April through early September, whereas Violet-crowned and Costa's nested during only a portion of this period.

The nesting of Costa's Hummingbirds in Guadalupe Canyon is believed to be a recent phenomena (Baltosser 1983). The fact that the species nests earlier to the west, and later in areas of sympatry (Stiles 1973, present study), may be due in part to competition as suggested by Cody (1974) for birds in general. Delayed nesting in Guadalupe Canyon may also result from the absence of nectar supplies prior to mid-April and the fact that subfreezing temperatures occasionally persist into April.

Violet-crowned Hummingbird nesting did not begin until mid-June, despite the fact that an occasional bird was present earlier. Late nesting by this species is believed to be related to its larger size (5.7 g) and subsequent need to perhaps specialize on more productive and predictable nectar resources, which did not become available until the second flowering period.

The occurrence of transient Broad-tailed and Rufous hummingbirds coincided with seasonal peaks in nectar abundance. Nectar availability in Guadalupe Canyon was highly contingent (Colwell 1974), i.e., nectar levels varied widely throughout the season but in a consistent temporal pattern each year. The result was that transients occurred during specific periods when nectar supplies happened to be greatest. Similar responses of hummingbirds to seasonal flushes in resource abundance have been shown by Gass (1979), DesGranges and Grant (1980), and Feinsinger (1980).

Spatial distribution of nesting species.—Segregation into different habitats is one of the most common means by which ecologically similar species partition resources (Schoener 1974). Nesting habitat selection by hummingbirds in Guadalupe Canyon was associated with the structure and exposure of the vegetation, with each species utilizing slightly different habitats for nesting. Black-chinned and Violet-crowned hummingbirds nested in habitats with many similar features, as did Broad-billed and Costa's hummingbirds.

The dispersion of hummingbird nests in Guadalupe Canyon was also associated with the spatial and temporal distribution of nectar supplies. When nectar supplies were not as evenly distributed throughout the canyon (i.e., during the first nesting period), segments having more abundant nectar supplies tended to have more nests. However, when nectar supplies were more evenly distributed (i.e., during the second nesting period),

segments having nectar supplies that were more predictable tended to have more nests. These results support the hypothesis that spacing patterns of species with altricial young should be correlated with the spatial and temporal distribution of food sources (Orians 1971).

Foraging and nectar availability.—Results of floral manipulations conducted on nectar supplies nearest the nests of Black-chinned, Broad-billed, and Violet-crowned hummingbirds in Guadalupe Canyon were similar to those conducted by Pimm (1978), from which the former were patterned. In Pimm's study, the Black-chinned was better able to cope with unpredictable nectar supplies than were larger Blue-throated Hummingbirds (*Lampornis clemenciae*). Black-chinned Hummingbirds (two adult females) in my study shifted their foraging to more distant agaves when nectar supplies were experimentally reduced. Whether this shift was in response to Broad-billed and Violet-crowned hummingbirds is not clear, as there were far more occasions in which individuals seemed to ignore the presence of another bird than instances that resulted in confrontation (e.g., a chase or calling). Violet-crowned and Broad-billed hummingbirds appeared to become somewhat more specialized when nectar was experimentally reduced, but nectar supplies nearest their nests were not sufficiently abundant so both also foraged at more distant agaves. For all three species, however, nectar supplies at outlying agaves seemed to be sufficiently abundant and yet close to have offset the effects of nectar reductions at the six agaves nearest nests.

Manipulations designed to reduce nectar availability during my study produced results that conform to *a priori* predictions in that hummingbirds: (1) showed measurable responses to reductions in nectar supplies, and (2) responded differently to these reductions. However, the final null hypothesis (i.e., reductions in nectar supplies will have no effect on nesting success) cannot be rejected. Foraging behavior of each hummingbird species in areas where nectar supplies nearest nests were reduced appeared to depend on the quantity, dispersion, and predictability of alternative nectar sources. As long as alternative supplies were nearby, predictable, and of sufficient quantities Black-chinned, Broad-billed, and Violet-crowned hummingbirds foraged from the same nectar sources. Only when nectar supplies were experimentally reduced did the Black-chinned make an obvious switch to alternative supplies and only during this period did the larger Violet-crowned appear to consistently dominate nectar sources nearest its nest.

Guild organization.—Patterns of seasonal occurrence, distribution, abundance, and interactions among guild members were not maintained indefinitely by any single factor, but were the result of several interdependent factors (Baltosser 1983). Unusual weather fluctuations, such as the record freeze that resulted in reduced foliage for nesting in 1980, may

on occasion have a substantial impact upon guild organization. In areas like Guadalupe Canyon, where each of the nesting species is at the periphery of its range, major weather fluctuations may assume added significance because these areas may experience "ecological crunches" (Wiens 1977) more frequently.

Small-scale differences in habitat selection and a partial seasonal separation of breeding seasons, the latter almost certainly predicated in part upon nectar availability, were important to guild organization. Periods of seasonal and daily abundance of nectar were interspersed with periods of limited availability. A major decline in availability during mid-June apparently influenced the number of individuals of each species that nested.

Patterns of organization in the Guadalupe Canyon hummingbird guild were similar to those in other studies of hummingbirds (e.g., Stiles 1973, Feinsinger 1976, DesGranges 1978, Feinsinger and Colwell 1978, Pimm 1978), and to nectarivorous guilds in general (e.g., Gill and Wolf 1975, Johnson and Hubbell 1975, Ford 1979). In Guadalupe Canyon the larger and more specialized Violet-crowned Hummingbird tended to utilize only the most productive and accessible nectar supplies, which it also tended to dominate, especially when these supplies were experimentally reduced. Smaller and more generalized species such as the Black-chinned and Broad-billed utilized many of the same nectar resources as the Violet-crowned, but unlike the Violet-crowned, both species also routinely utilized less productive and more highly dispersed sources. The potential effect on nesting of competition for nectar became apparent only when nectar supplies were experimentally decreased.

Thomson (1980) has suggested that evolutionary responses to competition may determine the attributes of species, while their numbers may respond to other pressures such as predation. The present study shows that nectar availability and habitat selection are each associated with, and important to, the organization of the Guadalupe Canyon hummingbird guild. Results support works such as Rotenberry (1978, 1980), Rotenberry et al. (1979), and Wiens (1974, 1977, 1983) that suggest that guilds are often not at resource-defined equilibrium. Guadalupe Canyon hummingbird populations appeared to be above equilibrium levels in 1976, nearer to such levels in 1977, and below these levels in 1980. The results of the present study, when coupled with other factors such as predation (Baltosser 1986), suggest that a variety of factors influence, perhaps intermittently, the structure of the Guadalupe Canyon hummingbird guild.

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LITERATURE CITED

- BALTOSSER, W. H. 1978. Ecological relationships among nesting hummingbirds in southwestern New Mexico and southeastern Arizona. M.S. thesis, New Mexico State Univ., Las Cruces, New Mexico.
- . 1983. Nesting ecology of sympatric hummingbirds in Guadalupe Canyon. Ph.D. diss., New Mexico State Univ., Las Cruces, New Mexico.
- . 1986. Nesting success and productivity of hummingbirds in southwestern New Mexico and southeastern Arizona. *Wilson Bull.* 98:353–367.
- BOLTEN, A. B., P. FEINSINGER, H. G. BAKER, AND I. BAKER. 1979. On the calculation of sugar concentration in flower nectar. *Oecologia* 41:305–315.
- CODY, M. L. 1974. Competition and the structure of bird communities. Monographs in Population Biology, No. 7. Princeton Univ. Press, Princeton, New Jersey.
- COLWELL, R. K. 1974. Predictability, constancy, and contingency of periodic phenomena. *Ecology* 55:1148–1153.
- CONNELL, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pp. 460–490 in *Ecology and evolution of communities* (M. L. Cody and J. M. Diamond, eds.). Belknap Press, Cambridge, Massachusetts.
- . 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131–138.
- DAVIES, N. B. AND A. LUNDBERG. 1985. The influence of food on time budgets and timing of breeding of the Dunnock *Prunella modularis*. *Ibis* 127:100–110.
- DESGRANGES, J. L. 1978. Organization of a tropical nectar-feeding bird guild in a variable environment. *Living Bird* 17:199–236.
- AND P. R. GRANT. 1980. Migrant hummingbirds' accommodation into tropical communities. Pp. 395–409 in *Migrant birds in the neotropics: ecology, behavior, distribution, and conservation* (A. Keast and E. S. Morton, eds.). Smithsonian Institution Press, Washington, D.C.
- DEUEL, B. AND T. PARKER. 1972. Costa's Hummingbirds in Guadalupe Canyon. P. 10 in *New Mexico Ornithol. Soc. Field Notes*, Vol. 11 (J. P. Hubbard, B. C. McKnight, and D. M. Niles, eds.). Cedar Crest, New Mexico.
- DIAMOND, J. M. 1978. Niche shifts and the rediscovery of interspecific competition. *Amer. Sci.* 66:322–331.
- DIXON, W. J. 1973. Biomedical computer programs. Health Sciences Computing Facility. Univ. California, Los Angeles, California.
- EWALD, P. W. AND S. ROHWER. 1982. Effects of supplemental feeding on timing of breeding, clutch-size and polygyny in Red-winged Blackbirds *Agelaius phoeniceus*. *J. Anim. Ecol.* 51:429–450.
- FEINSINGER, P. 1976. Organization of a tropical guild of nectarivorous birds. *Ecol. Monogr.* 46:257–291.

- . 1980. Asynchronous migration patterns and the coexistence of tropical hummingbirds. Pp. 411–419 in *Migrant birds in the neotropics: ecology, behavior, distribution, and conservation* (A. Keast and E. S. Morton, eds.). Smithsonian Institution Press, Washington, D.C.
- AND R. K. COLWELL. 1978. Community organization among neotropical nectar-feeding birds. *Amer. Zool.* 18:779–795.
- FORD, H. A. 1979. Interspecific competition in Australian honeyeaters: depletion of common resources. *Australian J. Ecol.* 4:145–164.
- GASS, C. L. 1979. Territory regulation, tenure, and migration in Rufous Hummingbird. *Can. J. Zool.* 57:914–923.
- GILL, F. B. AND L. L. WOLF. 1975. Economics of feeding territoriality in the Golden-winged Sunbird. *Ecology* 56:333–345.
- HAINSWORTH, F. R. AND L. L. WOLF. 1972. Crop volume, nectar concentration, and hummingbird energetics. *Comp. Biochem. Physiol.* 42A:359–366.
- IMMELMANN, K. 1971. Ecological aspects of periodic reproduction. Pp. 342–389 in *Avian Biology*, Vol. 1 (D. S. Farner, J. R. King, and K. C. Parkes, eds.). Academic Press, New York, New York.
- JAMES, F. C. AND H. H. SHUGART. 1970. A quantitative method of habitat description. *Amer. Birds* 24:727–736.
- JOHNSON, L. K. AND S. P. HUBBELL. 1975. Contrasting foraging strategies and coexistence of two bee species on a single resource. *Ecology* 56:1398–1406.
- KENDEIGH, S. C. 1944. Measurement of bird populations. *Ecol. Monogr.* 14:67–106.
- KNIGHT, R. L. 1988. Effects of supplemental food on the breeding biology of the Black-billed Magpie. *Condor* 90:956–958.
- LACK, D. 1954. *The natural regulation of animal numbers*. Oxford Univ. Press, London, England.
- MENGE, B. A. AND J. P. SUTHERLAND. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *Amer. Nat.* 110:351–369.
- MOREAU, R. E. 1950. The breeding seasons of African birds. *Ibis* 92:223–267.
- ORIAN, G. H. 1971. Ecological aspects of behavior. Pp. 513–546 in *Avian Biology*, Vol. 1 (D. S. Farner, J. R. King, and K. C. Parkes, eds.). Academic Press, New York, New York.
- PERRINS, C. M. 1970. The timing of birds' breeding seasons. *Ibis* 112:242–255.
- PIMM, S. L. 1978. An experimental approach to the effects of predictability on community structure. *Amer. Zool.* 18:797–808.
- POWERS, D. R. AND K. A. NAGY. 1988. Field metabolic rate and food consumption by free-living Anna's Hummingbirds (*Calypte anna*). *Physiol. Zool.* 61:500–506.
- ROBERTS, R. B. 1979. Spectrophotometric analysis of sugars produced by plants and harvested by insects. *J. Apicultural Res.* 18:191–195.
- ROTEBERRY, J. T. 1978. Components of avian diversity along a multifactorial climatic gradient. *Ecology* 59:693–699.
- . 1980. Dietary relationships among shrubsteppe passerine birds: competition or opportunism in a variable environment? *Ecol. Monogr.* 50:93–110.
- , R. E. FITZNER, AND W. H. RICKARD. 1979. Seasonal variation in avian community structure: differences in mechanisms regulating diversity. *Auk* 96:499–505.
- SCHOENER, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- STILES, F. G. 1973. Food supply and the annual cycle of the Anna Hummingbird. *Univ. Calif. Publ. Zool.* 97:1–109.

- STRONG, D. R., L. A. SZYSKA, AND D. S. SIMBERLOFF. 1979. Tests of community-wide character displacement against null-hypotheses. *Evolution* 33:897-913.
- THOMSON, A. L. 1950. Factors determining the breeding seasons of birds: an introductory review. *Ibis* 92:173-184.
- THOMSON, J. D. 1980. Implications of different sorts of evidence for competition. *Amer. Nat.* 116:719-726.
- WEATHERS, W. W. AND F. G. STILES. 1989. Energetics and water balance in free-living tropical hummingbirds. *Condor* 91:324-331.
- WIENS, J. A. 1974. Climatic instability and the "ecological saturation" of bird communities in North American grasslands. *Condor* 76:385-400.
- . 1977. On competition and variable environments. *Amer. Sci.* 65:590-597.
- . 1983. Competition or peaceful coexistence? *Nat. History* 1983 (3):30-34.
- WILLIAMS, A. B. 1936. The composition and dynamics of a beech-maple climax community. *Ecol. Monogr.* 6:317-408.
- WIMBERGER, P. H. 1988. Food supplement effects on breeding time and harem size in the Red-winged Blackbird (*Agelaius phoeniceus*). *Auk* 105:799-802.