

# BIRD VISITATION TO *AGAVE SALMIANA*: COMPARISONS AMONG HUMMINGBIRDS AND PERCHING BIRDS<sup>1</sup>

CARLOS MARTINEZ DEL RIO

Department of Zoology, University of Florida, Gainesville, FL 32611

LUIS E. EGUIARTE

Departamento de Ecología, Instituto de Biología, UNAM, Apdo. Postal 70-233, Coyoacan 04510, Mexico D.F.

**Abstract.** We studied bird visits to the flowers of *Agave salmiana* at two sites on the Mexican Plateau. At one site the main visitors were four species of perching birds (Northern Flicker, *Colaptes auratus*; Curve-billed Thrasher, *Toxostoma curvirostre*; Scott's Oriole, *Icterus parisorum*; and Northern Oriole, *Icterus galbula abeillei*) and one hummingbird, the Magnificent Hummingbird (*Eugenes fulgens*). At a second site, plants were visited by five species of hummingbirds (*E. fulgens*; White-eared Hummingbird, *Hylocharis leucotis*; Berylline Hummingbird, *Amazilia beryllina*; Violet-crowned Hummingbird, *Amazilia violiceps*; and Blue-throated Hummingbird, *Lampornis clemenciae*), and the Cinnamon-bellied Flowerpiercer, *Diglossa baritula*. At both sites, male *E. fulgens* defended inflorescences against other hummingbirds but not against perching birds. At one site, *E. fulgens* males defended inflorescences only in places with sparse vegetation; inflorescences located in areas with dense vegetation were visited by highly mobile nonterritorial hummingbirds. At both sites the numbers of birds in each inflorescence were a linear function of number of nectar-producing flowers. Arrival rates were also linearly related to flower numbers. For inflorescences with equal numbers of flowers, arrival rates were higher for hummingbirds than for perching birds. This resulted from the shorter residence times of the hummingbirds in the inflorescences. Different species of birds tended to use different parts of inflorescences.

**Key words:** *Nonspecialized nectarivory; hummingbirds; foraging behavior.*

## INTRODUCTION

Bat-pollinated plants have relatively open flowers (Faegri and van der Pijl 1971) and the nectar they produce, which is relatively accessible, is used by diurnal animals. Flowers of many Bombacaceae, like *Ceiba* spp. and *Pseudobombax* spp., and the large inflorescences produced by several species of *Agave* (Agavaceae) are used as sources of nectar by many species of birds (Baker et al. 1971; Stiles 1981; Kuban et al. 1983; Eguiarte et al., in press). In this paper we describe two contrasting assemblages of birds that visit flowers of cultivated, bat-pollinated *Agave salmiana* of the Mexican Plateau. We also describe the interactions and patterns of panicle utilization and partitioning that visiting birds show.

Inflorescences of *Agave* plants function as "patches" of concentrated resources for nectarivorous birds. These patches have unusually well-defined boundaries, and the quantities of resources they provide can be easily estimated (Howell 1979, Schaffer et al. 1979). The resource

availability in a patch determines how intensively it will be used relative to other patches (Fretwell and Lucas 1970, Harper 1982). We investigated the influence of patch (inflorescence) richness, measured as number of nectar-producing flowers, on number and visitation rates of birds.

## METHODS

### THE PLANT

*Agave salmiana* is one of the most widely cultivated agaves of the Mexican Plateau (Gentry 1982). It has been in cultivation for more than 5,000 years, and many of its characteristics have probably been molded by this long association with man (Callen 1965). Each plant produces at maturity a large paniculate inflorescence 6 to 8 m tall. The inflorescence has a central stalk with from 15 to 20 composite umbels in the upper half. The flowering period of *A. salmiana* spans the end of the dry season and the beginning of the rainy season (May to July), a period during which few other flowers are available to nectarivorous organisms. Nectar production is extremely high in flowers of *A. salmiana*. A group

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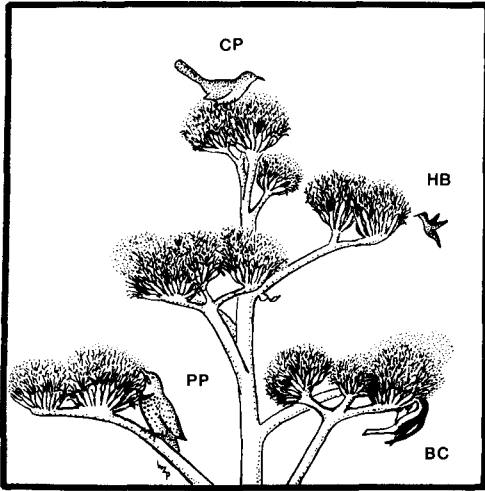


FIGURE 1. Diagrammatic representation of foraging positions used by birds feeding in *Agave* at site 1. CP = center of umbels perching, PP = perching in the peduncle of the umbel, BC = borders of the umbels clinging acrobatically from flowers, and HB = borders of the umbels hovering.

of 40 flowers from two individuals produced a mean volume of 101.6  $\mu$ l of nectar every 2 hr (SD = 47  $\mu$ l, 20 flowers per individual, six measurements per flower from 07:00 to 19:00). The rate of production remained constant throughout the day (M. del Rio and Eguiarte, unpubl.). Nectar sugar concentration was low (mean concentration  $\pm$  SD = 12.1 Brix  $\pm$  1.3,  $n$  = 240) as is typical of bat-pollinated flowers (Schaffer and Schaffer 1977).

#### STUDY SITES AND METHODS

We observed birds visiting *A. salmiana* during July and August 1983 at two sites: the botanical garden of the Instituto de Biología of the Universidad Nacional in the southern outskirts of Mexico City (site 1) and in a small valley located near km 24 of the Mexico-Cuernavaca highway (site 2), 8 km south of Presidio Sur, Distrito Federal.

In the botanical garden, observed inflorescences were part of an exhibition stand; in the small valley, plants were part of living fences separating abandoned fields. Both areas are surrounded by disturbed vegetation consisting of *Buddleia americana*, *Schinus molle*, *Quercus* spp., and abundant shrubs such as *Senecio* spp.

During summer 1983, 15 visits were made to site 1. Seven visits were made in the morning

(from 07:00 to 10:00) and eight in the afternoon (from 15:00 to 18:30). During these visits each observer chose an inflorescence at random and spent 3 hr recording all visits made by birds to flowers. For each visit, time spent in each of four foraging positions (see Results and Fig. 1 for a description) and total time in the inflorescence ("residence time") were recorded. All aggressive interactions observed were also recorded. The number of birds in each observed inflorescence was recorded in a 1-min census at 10-min intervals during the entire observation period. We visited site 2 on 10 mornings (from 07:00 to 11:30); the same observations described for site 1 were performed during these visits.

In order to estimate the number of open flowers in each observed inflorescence, all its umbels were numbered and mapped. During each observation period we recorded all flowering umbels and at the end of the flowering season we counted fruits and flower scars after cutting down the inflorescence.

#### RESULTS

The arrays of bird species visiting inflorescences were strikingly different in the two sites. Flowers in site 1 were visited by a diverse group of perching birds. Only one species of hummingbird, the Magnificent Hummingbird (*Eugenes fulgens*), was a common visitor at this site. Males of this species defended whole inflorescences as territories against other hummingbirds but not against perching birds. Other species of hummingbirds attempted to visit flowers, but defense was so effective that the majority of hummingbird visits recorded were by male *E. fulgens* (15% of the total number of visits). The most frequent visitor species to site 1 was the Northern Oriole (*Icterus galbula abeillei*) which contributed 62.2% of the 757 observed visits in 36 hr of observations. Scott's Oriole (*Icterus parisorum*), Northern Flicker (*Colaptes auratus*), and Curve-billed Thrasher (*Toxostoma curvirostre*) visited the flowers regularly but at lower frequencies (portions of total visits contributed by each of these species were 9.0%, 6.1%, and 5.2%, respectively). Species each contributing less than 2% of the total visits were: Berylline Hummingbird (*Amazilia beryllina*), White-eared Hummingbird (*Hylocharis leucotis*), and Blue Mockingbird (*Melanotis caerulescens*). No species of perching bird was observed defending territories at this site. Sizes of visitors at this site spanned

the range of previous reports of nectar-feeding birds (Fisk and Steen 1976, Brown et al. 1978).

At site 2 inflorescences were visited by five species of hummingbirds (*H. leucotis*; *A. beryllina*; Violet-crowned Hummingbird, *Amazilia violiceps*; *E. fulgens*; and Blue-throated Hummingbird, *Lampornis clemenciae*) and one species of perching bird, the Cinnamon-bellied Flowerpiercer (*Diglossa baritula*). Perching birds other than *D. baritula*, mainly *I. parisorum* and *I. g. abeillei*, were occasionally observed but were never recorded in a census. Of 736 visits observed in 20 hr, 41.0% were contributed by *E. fulgens*, 20.1% by *H. leucotis*, 16.1% by *D. baritula*, 10.2% by *A. violiceps*, 7.2% by *A. beryllina*, and 5.6% by *L. clemenciae*.

At site 2 some inflorescences were defended by *E. fulgens* males as exclusive territories against other hummingbirds. Defended inflorescences had variable numbers of flowers (ranging from 98 to 1,460 flowers,  $n = 14$ ) and appeared to be located in places where vegetation around the inflorescence was sparse; dense vegetation apparently precluded defense. Female *E. fulgens* and both sexes of *H. leucotis*, *A. beryllina*, and *A. violiceps* employed a highly mobile nonterritorial foraging behavior. *L. clemenciae*, the aggressively dominant species in this site (Table 1b), acted as a "large marauder" (sensu Feinsinger and Colwell 1978), foraging with impunity in both defended and nondefended inflorescences. *D. baritula* individuals defended inflorescences against conspecifics but not against hummingbirds. Territorial defense was independent of vegetation cover and we never observed more than one individual per inflorescence (except during intrusions and chases).

Aggressive displacements observed at site 1 and at nonterritorial inflorescences in site 2 are shown in Tables 1a and 1b. At both sites an interspecific dominance hierarchy existed in which larger species were dominant over smaller ones. Level of aggression was much higher in the assemblage dominated by hummingbirds (87 aggressions in 36 hr at site 1 versus 284 aggressions in 20 hr at site 2). No aggressions were ever recorded among perching birds and hummingbirds at either site.

For inflorescences that were not defended by male *E. fulgens* at site 2 and for all inflorescences at site 1, a significant linear relationship was found between mean number of birds counted at 10-min intervals during the observation period and

TABLE 1. Aggressive encounters between visiting species.

Table 1a.—Site 1

|                                 | Loser |      |      |      |      | Other hummingbirds |    |
|---------------------------------|-------|------|------|------|------|--------------------|----|
|                                 | C.a.  | T.c. | I.p. | I.g. | E.f. |                    |    |
| Winner                          | C.a.  | 1    | 1    | 0    | 2    | 0                  | 0  |
|                                 | T.c.  | 0    | 0    | 0    | 18   | 0                  | 0  |
|                                 | I.p.  | 0    | 0    | 0    | 12   | 0                  | 0  |
|                                 | I.g.  | 0    | 0    | 0    | 24   | 2                  | 0  |
|                                 | E.f.  | 0    | 0    | 0    | 0    | 12                 | 15 |
| Total aggressions in 36 hr = 87 |       |      |      |      |      |                    |    |

C.a. = *Colaptes auratus*, T.c. = *Toxostoma curvirostre*, I.p. = *Icterus parisorum*, I.g. = *Icterus galbula abeillei*, E.f. = *Eugenes fulgens*. Other hummingbirds = *Amazilia beryllina* and *Hylocharis leucotis*.

Table 1b.—Site 2

|                                  | Loser |      |      |      |      |      |    |
|----------------------------------|-------|------|------|------|------|------|----|
|                                  | L.c.  | E.f. | A.v. | A.b. | H.l. | D.b. |    |
| Winner                           | L.c.  | 0    | 7    | 5    | 0    | 12   | 0  |
|                                  | E.f.  | 0    | 65   | 19   | 14   | 85   | 0  |
|                                  | A.v.  | 0    | 13   | 0    | 0    | 9    | 0  |
|                                  | A.b.  | 0    | 0    | 2    | 0    | 15   | 0  |
|                                  | H.l.  | 0    | 0    | 1    | 7    | 11   | 0  |
|                                  | D.b.  | 0    | 0    | 0    | 0    | 0    | 19 |
| Total aggressions in 20 hr = 284 |       |      |      |      |      |      |    |

L.c. = *Lampornis clemenciae*, E.f. = *Eugenes fulgens*, A.v. = *Amazilia violiceps*, A.b. = *Amazilia beryllina*, H.l. = *Hylocharis leucotis*, D.b. = *Diglossa baritula*.

the number of nectar-producing flowers in each inflorescence ( $y = 0.31 + 0.00095x$ ,  $r = 0.98$ ,  $n = 12$  and  $y = -0.21 + 0.00272x$ ,  $r = 0.88$ ,  $n = 10$  for site 1 and 2 respectively, see Fig. 2). Mean number of bird arrivals per 10-min interval and number of flowers were also related in a linear fashion ( $y = 1.65 + 0.0028x$ ,  $r = 0.86$ ,  $n = 13$  and  $y = 2.06 + 0.0234x$ ,  $r = 0.87$ ,  $n = 16$  for site 1 and 2 respectively, see Fig. 2).

For inflorescences with >300 flowers, the point at which regressions of mean numbers of birds versus numbers of flowers for the two sites intersected, the number of birds per inflorescence was greater at site 2 than at site 1 (i.e., there were more hummingbirds than perching birds for inflorescences of equal numbers of flowers). Visitation rates were higher for all numbers of flowers per inflorescence in the hummingbird-dominated community (ANCOVA for intercepts and slopes;  $F = 79.72$  and  $F = 45.27$  respectively,  $P < 0.001$  in both cases).

Hummingbirds tended to make shorter visits to inflorescences than did perching birds (Table 2), and at site 1 a positive correlation between residence time and body size existed. Residence

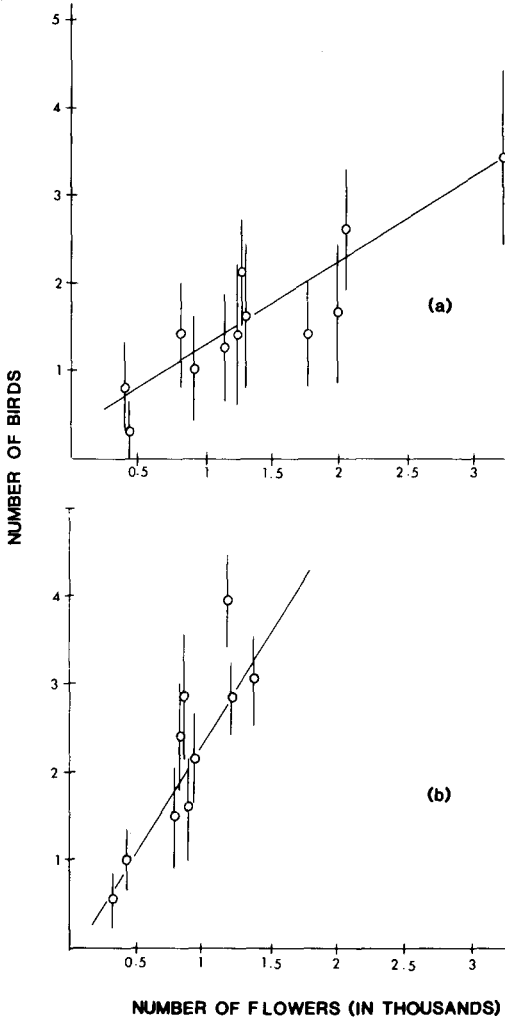


FIGURE 2. Relationship between mean number of birds feeding in inflorescences and number of nectar-producing flowers for sites 1 (a) and 2 (b). Each point is the mean of 16 1-min counts made at 10-min intervals, bars are standard deviations.

time for *E. fulgens* varied between sexes. Territorial males in site 1 made significantly shorter visits than females ( $t = 4.03$ ,  $P < 0.005$ ). The difference in residence times between territorial males at site 1 and site 2 was not significant ( $t = 1.64$ ,  $P = 0.20$ ).

Different foraging positions used by birds feeding in agave at site 1 are shown in Figure 2. Proportions of time spent foraging in each position differed among the five species (Table 3). The larger species (*C. auratus* and *T. curvirostre*)

TABLE 2. Time spent in the inflorescence per visit.

| Species                                       | Mean residence time $\pm$ SD (sec) | n  |
|---|------------------------------------|----|
| <i>Colaptes auratus</i> <sup>a</sup>          | 468 $\pm$ 186                      | 11 |
| <i>Toxostoma curvirostre</i> <sup>a</sup>     | 644 $\pm$ 279.6                    | 7  |
| <i>Icterus parisorum</i> <sup>a</sup>         | 176 $\pm$ 78.0                     | 15 |
| <i>Icterus galbula abeillei</i> <sup>a</sup>  | 141 $\pm$ 55.8                     | 30 |
| <i>Eugenes fulgens</i> (males) <sup>a</sup>   | 20.4 $\pm$ 9.6                     | 17 |
| <i>Hylocharis leucotis</i> <sup>b</sup>       | 23.1 $\pm$ 12                      | 24 |
| <i>Amazilia beryllina</i> <sup>b</sup>        | 46.7 $\pm$ 24.3                    | 9  |
| <i>Amazilia violiceps</i> <sup>b</sup>        | 17.6 $\pm$ 10.5                    | 16 |
| <i>Eugenes fulgens</i> (males) <sup>b</sup>   | 15.5 $\pm$ 6.8                     | 15 |
| <i>Eugenes fulgens</i> (females) <sup>b</sup> | 42.8 $\pm$ 26.5                    | 26 |

<sup>a</sup> Site 1.

<sup>b</sup> Site 2.

preferentially used the center of umbels. *Icterus parisorum* used both umbel centers and the border adjacent to peduncles in almost equal proportions. *Icterus g. abeillei* used mainly flowers on borders of umbels while clinging to them acrobatically. *Icterus g. abeillei* individuals were the only perching birds at this site capable of "sucking" nectar without tilting up their heads to swallow (cf. Moermond 1981). Among perching-bird species, this ability probably gave them the exclusive use of the flowers at the edge of umbels, because these flowers demanded feeding acrobatically in positions that preclude head-tilting. At this site *E. fulgens* males visited flowers mainly in flight, although they sometimes perched in the perianth of flowers while feeding. At site 2 all species of hummingbirds appeared to use the same parts of the umbels in a similar manner, using only flowers at edges and avoiding the "forest" of stigmas and stamens at the center. The small size of *D. baritula* precluded a detailed quantitative analysis of sites used by this species while foraging. However, examination of the perforations left at the base of flowers by these birds showed that they were preferentially perforating flowers toward the center of the umbels.

## DISCUSSION

### DIFFERENCES IN ASSEMBLAGE COMPOSITION

The striking differences in species composition found between sites 1 and 2 is puzzling and we do not have an adequate explanation for it. Site 1 is located in a 300-ha island of natural vegetation that is surrounded by urban development. The species composition of the *A. salmiana* visitors has been monitored for several years and appears to be constant (M. del Rio, Eguiarte, and

TABLE 3. Proportions of time spent in each foraging position at site 1.

| Species                         | CP   | PP   | BP   | HB   | Time* (min) | No. of observations |
|---------------------------------|------|------|------|------|-------------|---------------------|
| <i>Colaptes auratus</i>         | 0.96 | 0.04 | 0    | 0    | 44.3        | 5                   |
| <i>Toxostoma curvirostre</i>    | 0.86 | 0.14 | 0    | 0    | 74.7        | 7                   |
| <i>Icterus parisorum</i>        | 0.45 | 0.54 | 0    | 0    | 43.4        | 15                  |
| <i>Icterus galbula abeillei</i> | 0.17 | 0.11 | 0.72 | 0    | 195.4       | 80                  |
| <i>Eugenes fulgens</i> (males)  | 0    | 0    | 0.18 | 0.82 | 9.5         | 25                  |

\* Pooled total time for all the birds observed. CP = Center of umbels perching, PP = perching in the peduncle of the umbels, BC = borders of the umbels clinging acrobatically, and HB = borders of the umbels hovering.

Burquez, unpubl.). Most of the species of hummingbirds that use *A. salmiana* flowers at site 2 are also present in the area surrounding site 1. Their absence from inflorescences can be best explained by the effectiveness of *E. fulgens* males in chasing other hummingbirds away. All the species of perching birds that use *A. salmiana* at site 1 were seen or heard on various occasions in site 2. With the exception of sporadic visits by orioles, these species did not visit the inflorescences. Ford's (1985) summary of the records of flower visits by birds in Europe suggests that if the nectar-dispensing plants are available, many species of normally nonnectarivorous species will utilize nectar opportunistically. It may be that quantitative differences in species composition can account for the differences between the two sites.

#### AGGRESSION AND TERRITORIALITY

Moore (1978) and Murray (1981) have suggested that interspecific aggression should be directed only toward other species that use the same resources and are potential competitors. Under most circumstances orioles, flickers, and thrashers do not use the same resources as hummingbirds. It is likely that neither perching birds nor hummingbirds recognize each other as competitors, even when they are actually competing for nectar in *A. salmiana* flowers (*E. fulgens* and *I. g. abeillei* largely use the same flowers). The paucity of aggressive interactions between these two groups lends support to this interpretation. At site 2 we never recorded aggressive encounters between hummingbirds and *D. baritula*. Flowerpiercers fed preferentially in flowers at the center of umbels and were probably not detected by hummingbirds. Hummingbirds and flowerpiercers (*Diglossa*) are potential competitors at other flower species, but the degree of mutual aggressiveness they show seems to be small and considerably less than that shown among hum-

mingbird species (Moynihan 1968, Lyon and Chadek 1971, Colwell et al. 1974).

The comparatively higher aggression levels at site 2 relative to site 1 can be explained by the higher densities of birds per inflorescence at site 2 (for inflorescences larger than 300 flowers) rather than by the hummingbirds being more aggressive than perching birds. Higher densities of birds presumably increase the probability of random encounters and, thus, of aggression.

Dense vegetation appeared to preclude territorial defense by *E. fulgens* males at site 2 (at site 1 all inflorescences were located in open "habitats"). Nonterritorial birds formed small aggregations that hid in the vegetation below the inflorescences. These birds opportunistically filched nectar while the bird attempting to defend the inflorescence chased other intruders. During the study period we observed male *E. fulgens* attempting to establish territories in inflorescences surrounded by vegetation. On all these occasions the territorial birds gave up after a short period as a result of repeated intrusions by birds that hid in the vegetation below. Vegetation cover decreases the detectability of intruders, favors formation of small groups that can "mob" territory holders, and reduces effectiveness with which holders can chase intruders away (Moore 1978). Snow and Snow (1984) observed that *Turdus viscivorus* defended only free-standing fruiting trees, and Kuban et al. (1983) reported that the Ruby-throated Hummingbird (*Archilochus colubris*) established territories in inflorescences of *A. havardiana* only in open habitats.

#### DENSITY RESPONSES TO PATCH RICHNESS

The linearity of the relationships between mean bird density and flower number per inflorescence indicates that the ratio of the number of birds relative to the number of flowers remained relatively constant for all inflorescence richness. The distribution of birds in the assemblage of inflo-

rescences resembled what Fretwell and Lucas (1970) have called an "ideal free distribution." Parker and Sutherland (1986) have suggested that ideal free-like distributions of individuals among patches can be achieved even when individuals differ in competitive ability. This result holds when competitive differences between individuals remain constant across patches and input of resources to each patch is constant. These assumptions seem to be fulfilled by the *Agave*-visitor system.

Number of birds present in an inflorescence at any given time represented a dynamic equilibrium between number of arrivals and number of departures. At equilibrium, therefore, number of arrivals per unit time is a measure of "turnover rate" of individuals at the inflorescence. Arrival rates were much higher at site 2 than at site 1 as a result of hummingbirds making shorter visits. Residence time is, in broad terms, positively correlated with body size. The turnover rates of individuals in patches are, therefore, influenced by body size of the species composing the assemblage of visitors. Assemblages composed of small-sized species are apparently more dynamic and have higher turnover rates than those composed of big species.

#### PATTERNS OF PANICLE PARTITIONING

Patterns of panicle use shown by both assemblages of birds are good examples of how accidental and presumably transient ecological relationships can result in complex and precisely-patterned communities. Places where birds fed and the mode in which they visited flowers at site 1 were clearly determined by the morphological characteristics of each species and by the dominance hierarchy of the assemblage. Heavy perching birds were forced to feed at those places that had suitable perches, such as the center of umbels and flowers near peduncles. *Icterus g. abeillei* individuals were forced to use flowers near the borders of the umbels by the combined effects of the other three competitively dominant species. Among the nonhovering birds, *I. g. abeillei* had the exclusive use of the border flowers because it was able to forage acrobatically.

At site 2 hummingbirds were unable to penetrate the forest of stamens and stigmas, and were therefore unable to use flowers at the center of the umbels. *Diglossa baritula* used these flowers preferentially presumably because they had not been depleted of nectar by hummingbirds. Bird

visitation to *A. salmiana* is possibly a phenomenon of recent origin. Most bat-pollinated agaves have reduced diurnal nectar production (Schaffer and Schaffer 1977). It is likely that the copious nectar that *A. salmiana* produces during the day is a by-product of human selection for increased sap production. Patterns of resource partitioning shown by the assemblages of visitors, therefore, cannot be attributable to close coevolution. Our data suggest that these patterns are largely determined by the combined effects of morphological limitations and behavioral interactions.

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