



Nectar oasis produced by *Agave marmorata* Roezl. (Agavaceae) lead to spatial and temporal segregation among nectarivores in the Tehuacán Valley, México

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We investigated temporal and spatial segregation of nectarivores at *Agave marmorata* inflorescences in Tehuacán, México. Using survival analysis, a technique in which data are treated as censored, we found temporal segregation among insects, hummingbirds, and perching birds during the most nectar-limited time. Survivorship curves of hummingbirds and orioles were not significantly different from each other, however, temporal segregation was observed within hummingbirds according to body size and territorial behavior. Temporal segregation among hummingbirds is interpreted as a way to reduce risk of injury. This way hummingbirds meet their short-term energy demands and co-existence may be facilitated in a nectar oasis. In contrast, survivorship curves of oriole species were not statistically different with each other, but spatial segregation is suspected; Scott's Orioles segregate by visiting agaves with taller inflorescences sooner than visiting those with shorter inflorescences. These results along with those of foraging behavior and floral shifts suggest that orioles are the legitimate pollinators of this century plant.

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Introduction

Nectarivorous assemblages typically composed by either bees, hawkmoths, hummingbirds, passerine birds, and/or bats sharing resources over time, have been widely documented in the literature (Alcorn *et al.*, 1961; Lyon & Chadek, 1971; Borrero, 1972; Primack & Howe, 1975; Cruden & Toledo, 1977; Toledo, 1977; Boyden, 1978; Des Granges, 1978; Carpenter, 1979; Feinsinger *et al.*, 1979; Hernández & Toledo, 1979, 1982; Morton, 1979; Schaffer *et al.*, 1979; Steiner, 1979; Kodric-Brown & Brown 1979; Toledo & Hernández, 1979; Gill *et al.*, 1982; Kuban *et al.*, 1983;

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Schluter, 1986; Eguiarte & Búrquez, 1987; Eguiarte *et al.*, 1987; Martínez del Rio & Eguiarte, 1987; Gryj *et al.*, 1990; Westerkamp, 1990; Sazima *et al.*, 1993; Sazima & Buzato, 1994; Buzato *et al.*, 1994; Fleming *et al.*, 1996). Researchers have concentrated most of their attention on describing how distantly related taxa partition nectar resources and describing their role as pollinators.

In this paper, we present data from a diverse and distantly related assemblages of nectarivores feeding from century plants, but focused on the relative importance of temporal segregation during the most nectar-limited time in the semi-arid Tehuacán Valley. This study is a starting point to generate hypotheses about the processes affecting the structure of this community of nectarivores.

Methods

Study site

The study was carried out in the Tehuacán Valley (18°20'N, 97°28'W; at 1700 m a.s.l.), Puebla, México. Data were collected in May of 2000 near the city of Tehuacán (km 48 Puebla-Oaxaca 135 road), in a flat, rocky area dominated by *Yucca periculosa*, *Agave marmorata*, *Euphorbia antisiphylitica*, *Opuntia pilifera*, *Pachycereus hollianus*, *Myrtillocactus geometrizans*, *Acacia constricta*, *Mimosa luisana*, and *Prosopis laevigata* (Dávila *et al.*, 1995). The region owes its aridity to the rain shadow produced by the Eastern Sierra Madre (Smith, 1965). Most rain occurs during summer time (Dávila *et al.*, 1995). It has an average rainfall of 400 mm, an annual mean temperature of 21°C, and rarely freezes (García, 1973). The main vegetation type is an arid tropical scrub ('matorral xerófilo'; Rzedowski, 1978) in which succulent forests of columnar cacti with densities of up to 1200 individuals ha⁻¹ constitute dominant elements in some areas of the valley (Valiente-Banuet & Ezcurra, 1991). Avifauna is composed by a mix of species typically distributed along the Chihuahuan and Sonoran Deserts that have their southernmost distribution in the Tehuacán Valley, endemics to the Balsas drainage and the Tehuacán-Cuicatlán Valley, and local migrants from adjacent tropical deciduous forests and pine-oak woodlands to the Tehuacán Valley (Arizmendi & Espinosa de los Monteros, 1996).

Most columnar cacti provide birds and bats with nectar in the spring (more than 50% of potential reproductive individuals are flowering by April; Valiente-Banuet *et al.*, 1997; J. García, *pers. comm.*), and depend on them for pollination and seed dispersal (Valiente-Banuet *et al.*, 1996, 1997). Later in the year, when nectar resources from columnar cacti run out, agaves may help to maintain the resident bat population (85% of 19 agave species flower between June and November; Dávila *et al.*, 1995; S. Arizaga, unpublished data). Flowering of *A. macroacantha* spans from June to July (Arizaga, 2000) and in some areas coexist with *A. marmorata* (S. Arizaga, *pers. comm.*). During our study (May), the only major species that flowered was *Agave marmorata* (Agavaceae). Alternate resources during this time of year include bee-pollinated *Opuntia pilifera* (Cactaceae) and hummingbird-pollinated *Pedilanthus cymbiferus* (Euphorbiaceae), but the amount of nectar offered is minimal (J. F. Ornelas, *pers. obs.*). Therefore, the nectar that is offered by agaves between late April and early June (J. García, *pers. comm.*) represents a nectar oasis to nectar-feeding animals.

Study species

Agave marmorata Roezl. is a frost-sensitive, obligately outcrossed, semelparous, large agave belonging to the subgenus *Agave*, group Marmoratae (Gentry, 1982). Commonly found in semi-arid areas in Central México (Puebla and Oaxaca),

A. marmorata is characterized by a grayish marble-like hue and scabrous leaves (100–135 cm) with crenate margins and small terminal spines (Gentry, 1982). At the end of its life cycle, each rosette produces a ≈ 6 -m paniculate inflorescence. The inflorescence has a central stalk branching with 20–25 large diffuse decompose umbels in upper half of the shaft (Gentry, 1982). The bright yellow flowers with small tubes (14–16 mm; M. Ordano, unpublished data) are protandrous and flower characteristics suggest bat pollination (Faegri & Van der Pijl, 1971; Gentry, 1982). Flowers (tubes 5–6 mm deep and 12 mm wide; Gentry, 1982) are open four days and, if not pollinated abscise by the sixth day. On the first day, the style is very short (mean \pm S.E. = 45.33 ± 1.03 mm, $n = 61$ flowers), and the stigmatic lobes are closed. By late afternoon, stamens are fully extended (mean \pm S.E. = 69.63 ± 0.54 mm, $n = 61$) and anthers open offering large amounts of yellow pollen until the end of the next day. By the end of the second day, the style grows beyond the stamens (mean \pm S.E. = 85.33 ± 1.43 mm, $n = 61$) and the stigmatic surface begins to open. Anther dehiscence occurs ≈ 24 h prior to stigma receptivity (M. Ordano, *pers. obs.*). Stigmas are receptive during day hours of the second day and the receptivity increases over the day. The proportion of receptive stigmas range from 17 to 20 early in the day (0700–1000) and from 50 to 80 in the afternoon (1300–1600); most stigmas become receptive by 2300 (M. Ordano, unpublished data). Standing pollen crops were higher in morning hours (31% of stamens shedding pollen), decreased by midday (10%), then increased at night (58%). More pollen is available at night and the decrease by mid-afternoon matches the increase in stigma receptivity (50% of receptive stigmas) (M. Ordano, unpublished data). Although nectar production is higher at night ($576.61 \mu\text{l flower}^{-1} 12 \text{ h}^{-1}$; Benítez *et al.*, 1998), flowers produce considerable amounts of nectar over the day. During day hours, standing nectar crops range from 0.2 to 1.14 ml flower⁻¹ and sugar concentration from 9% to 37% (BRIX) (M. Ordano, unpublished data). Staminate flowers produce more nectar and more concentrated than pistillate flowers (Benítez *et al.* 1998; M. Ordano, unpublished data). Pollen and nectar-feeding bats and sphingid moths have been observed using flowers of *A. marmorata* (Rojas-Martínez & Valiente-Banuet, 1996; A. Rojas-Martínez, *pers. comm.*). Diurnal floral visitors presumably use the remnant nectar that is not consumed by nocturnal visitors (Slauson, 2000). Legitimate pollinators are unknown. The flowering period of *A. marmorata* spans from end of the dry season (May) to the beginning of the rainy season (June). In 2001, individuals of *A. marmorata* flowered earlier in the year (March–May) (J. F. Ornelas, *pers. obs.*).

Temporal patterns of visitation

We haphazardously selected 10 out of the only 35 flowering agaves available in the study area (≈ 100 ha) to observe floral visitors over the course of a day (May 1, 2000). For each plant, we recorded every single foraging event throughout the observation period (0930–1630; 70 h of sampling effort), and noted the species, time of day, foraging behavior, and aggressive interactions. Data were also collected on animals to determine their role as pollinators; the most likely to transfer pollen from one flower to the receptive stigma of another. Observations were performed ≈ 10 m away from the focal inflorescence. Approach and avoidance behavior by birds was not detected during observations. Visits by nectar feeding bats and sphingid moths were brief but we were able to determine by visual observation (or binoculars) whether stigma contact was made. Nocturnal observations were made very close to the plants and directing a light source to the umbels.

We used Survival Analysis (also known as ‘failure time analysis’) to explore temporal segregation among nectarivores (Abacus Concepts, Inc., 1996). One of the advantages of using survival analysis is that allows for use of censored data. Censored

data points are those in which an event has not been observed because the study ended before the event could have happened to some of the individuals under observation (Muenchow, 1986; Fox, 2001). This feature is apt to be useful in field biology, where the observation period may be too brief for all possible events to occur (Muenchow, 1986; Pyke & Thompson, 1986), but it has rarely been used in this context (Fox, 2001).

We recorded the beginning of our observations as time zero and subsequent foraging events as minutes from start time. The event for each monitored agave was the visit of all possible nectarivores for the duration of our study. If an event occurred for a given plant, then it became uncensored data, and if it never occurred, then it became censored data. We then used the Kaplan–Meier product-limit nonparametric method for the computation of functions among variables and the logrank (Mantel–Cox) statistic to test for differences among groups with the same taxonomic affiliation and species within them. In our case, ‘survivorship’ was the probability that a species or group of species had not yet visited an agave a given number of minutes after the start of observation.

Based on our preliminary observations, we expected for each individual agave the visit of *Xylocopa*, bees, hummingbirds, and passerines (see Results). Non-identified insects, *Apis mellifera*, and *Bombus* sp., were observed foraging throughout the day. We only followed individual visits of *Xylocopa* sp. *Bombus* visits were not followed because they are too small to pollinate. We counted honeybees every hour by counting for one minute the number of them flying around the lowest flowering umbel of each focal plant (mean \pm S.E. = 7.57 ± 0.82 honeybees flowering umbel⁻¹ min⁻¹), however, we were unable to follow them individually within hours. Large numbers of honeybees may have important effects on the structure of the nectarivore community, but we believe little pollination is performed due to their small size and foraging habits (see also Slauson, 2000). We used this rationale for excluding honeybee observations and, therefore, not analysed any further.

At the end of our observations, we counted the number of flowering umbels and measured inflorescence height from the ground (m) and the distance to the closest flowering conspecific (m) on each of the focal plants. We then correlated these characteristics (Spearman Rank Correlation) with the number of visits, and used them as covariates to explore spatial segregation.

Foraging modes and pollination

Foraging behavior of floral visitors was observed in two subsequent days (May 2 and 3, 2000) directly or through binoculars. The frequency and the mode of flower exploitation were recorded for each type of visitor during 30-min intervals at 0700, 1000, 1300, and 2300. We categorized foraging behaviors as follows: (1) hovering, (2) clinged to the perianth of the flower, (3) perched at the peduncle of the umbel, and (4) perched on top of the umbel. We also noted whether visitors would move from umbels containing mostly staminate flowers to umbels containing both staminate and pistillate flowers while feeding on agave flowers, and whether they contacted anthers and pollen during a foraging bout.

Results

Floral visitors

We observed 15 species of birds feeding on *A. marmorata* flowers: *Cynanthus sordidus* (Gould) (Dusky Hummingbird), *C. latirostris* Swainson (Broad-billed Hummingbird),

Amazilia violiceps (Gould) (Violet-crowned Hummingbird), *Lampornis clemenciae* (Lesson) (Blue-throated Hummingbird), *Eugenes fulgens* (Swainson) (Magnificent Hummingbird), *Calothorax pulcher* Gould (Beautiful Hummingbird), *Melanerpes hypopolius* (Wagler) (Gray-breasted Woodpecker), *Campylorhynchus jocosus* Sclater (Boucard's Wren), *Mimus polyglottos* (Linnaeus) (Northern Mockingbird), *Toxostoma curvirostre* (Swainson) (Curve-billed Thrasher), *Icterus wagleri* Sclater (Black-vented Oriole), *I. spurius* (Linnaeus) (Orchard Oriole), *I. pustulatus* (Wagler) (Streak-backed Oriole), *I. parisorum* Bonaparte (Scott's Oriole), and *Carpodacus mexicanus* (Müller) (House Finch).

A total of 586 foraging events were registered during our study (*Xylocopa* = 43, hummingbirds = 294, and perching birds = 249). We observed 7.81 ± 0.9 (mean \pm S.E.) bird visits $\text{plant}^{-1} \text{h}^{-1}$ and ≈ 1 *Xylocopa* (mean \pm S.E. = 0.96 ± 0.11 visits $^{-1} \text{plant}^{-1} \text{h}^{-1}$) (Fig. 1). Birds were more active visiting agave inflorescences at early hours (14.8 ± 3.8 birds $\text{plant}^{-1} \text{h}^{-1}$). Hummingbirds were relatively more frequent in the morning and perching birds in the afternoon (Fig. 1). Pollen and nectar-feeding bats, *Choeronycteris mexicana* Tschudi and *Leptonycteris nivalis* (Saussure) and sphingids were confirmed to be using *A. marmorata* flowers at night.

Hummingbirds accounted for 50.2% of the foraging events observed on *A. marmorata*, 42.5% for perching birds and 7.3% for *Xylocopa* sp. Six species of hummingbirds (*E. fulgens*, *C. pulcher*, *C. latirostris*, *A. violiceps*, *C. sordidus*, and *L. clemenciae*) were recorded during observations, and the contribution of each species to the total number of foraging events was not evenly distributed (14.2%, 14.0%, 10.6%, 8.5%, 2.6%, and 0.3%, respectively). Orioles (*I. parisorum*, *I. pustulatus*, and *I. wagleri*) were the most abundant perching birds feeding on *A. marmorata* (39.1%) and *M. hypopolius*, *C. jocosus*, *M. polyglottos*, and *C. mexicanus* accounted for the remaining foraging events (3.4%). *T. curvirostre* and *I. spurius* were not detected during foraging observations.

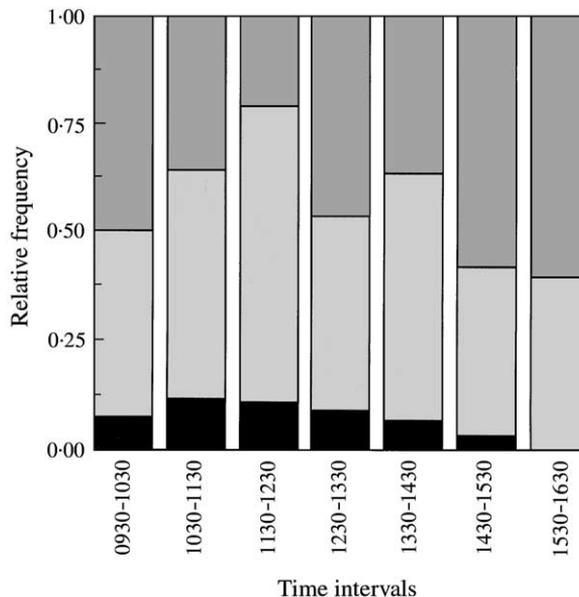


Figure 1. Relative frequency of floral visitors over time in *Agave marmorata*. *Xylocopa* (■); Hummingbirds (□); Perching birds (▒).

Temporal segregation among insects, hummingbirds, and perching birds

The number of observations was 654 (*Xylocopa* = 44, hummingbirds = 314, perching birds = 249), and 68 observations were censored data (*Xylocopa* = 1, hummingbirds = 20, perching birds = 47). We found significant differences among survivorship curves of *Xylocopa*, hummingbirds, and perching birds ($\chi^2 = 22.48$, df. = 2, $p < 0.0001$; Fig. 2), suggesting that the time until a *Xylocopa* arrived to an agave is shorter (≈ 100 min) than the time for hummingbirds (≈ 150 min) and perching birds (≈ 200 min). Because more than 20% of *M. hypopolius*, *C. jocosus*, *M. polyglottos*, and *C. mexicanus* foraging events were censored, these were eliminated from a subsequent analysis ($n = 20$ foraging events) as recommended by Pyke & Thompson (1986). *Xylocopa* sp. was also eliminated from further analyses given the small number of foraging events. We then categorized our foraging data ($n = 523$ foraging events) as either hummingbird ($n = 294$) or oriole visits ($n = 229$), and found no differences among them ($\chi^2 = 0.004$, df. = 1, $p = 0.9504$; Fig. 3).

Temporal segregation within hummingbirds

A total of 277 foraging events of hummingbirds were considered in this exploratory analysis (*C. latirostris* = 62, *A. violiceps* = 50, *E. fulgens* = 83, *C. pulcher* = 82). Species with small sample sizes ($n = 17$ foraging events) were not included (*L. clemenciae* = 2, *C. sordidus* = 15). We found significant differences among hummingbird species ($\chi^2 = 9.84$, df. = 3, $p < 0.05$; Fig. 4(a)), and agaves were visited sooner by territorial, medium-sized (5.3 g; Ornelas, 1995) hummingbirds *A. violiceps* (≈ 100 min), and then by smaller hummingbirds (3.1 g; Ornelas, 1995) *C. latirostris* (≈ 160 min), and *C. pulcher* (2.7 g; Ornelas, 1995; ≈ 210 min). The most frequent and largest hummingbird *E. fulgens* (7.5 g; Ornelas, 1995) acted as a "large marauder" (*sensu* Feinsinger & Colwell, 1978), foraging with impunity through the day.

Temporal segregation within orioles

A total of 229 foraging events of orioles were registered during our study (*I. parisorum* = 201, *I. pustulatus* = 22, *I. wagleri* = 6). Survivorship curves were

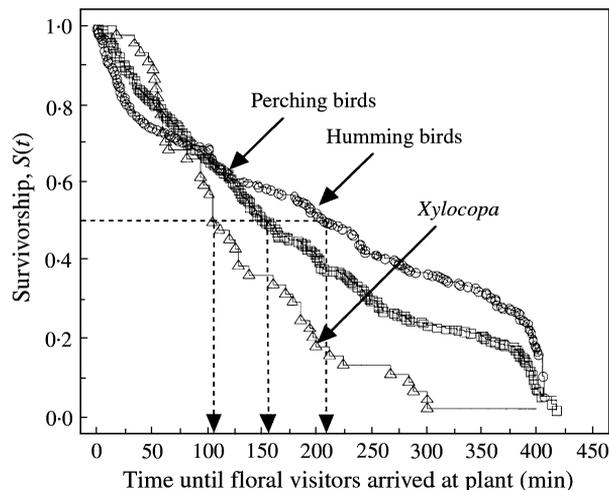


Figure 2. Nonparametric survival functions showing visitation of diurnal floral visitors in *Agave marmorata*.

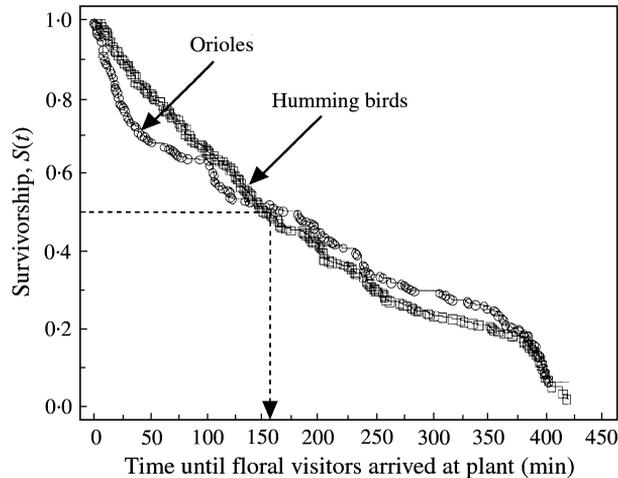


Figure 3. Nonparametric survival functions showing visitation of hummingbirds and orioles in *Agave marmorata*.

significantly different within orioles ($\chi^2 = 21.44$, $df. = 2$, $p < 0.0001$; Fig. 5(a)), however, because the smallest oriole (*I. spurius*) was not detected during our observations and sample sizes were small for *I. wagleri* and *I. pustulatus*, data regarding temporal segregation within orioles must be taken with caution.

Spatial segregation

To determine whether temporal segregation was explained by the intrinsic plant characteristics, we looked at the variation in the number of visits as a function of such characteristics (Table 1). Agaves were separated from the closest flowering conspecific by less than 10 m (mean \pm S.E. = 18.2 ± 9.04 m) and had a paniculate inflorescence of 5.71 ± 0.45 m in height with 11.00 ± 0.85 flowering umbels (Table 1). Plants received in average 65 visits (65.4 ± 3.4 ; Table 1). Variation among plants in the number of visits they received by *Xylocopa*, hummingbirds, and perching birds ranged from 17 to 128. In average, each plant received four *Xylocopa* visits (mean \pm S.E. = 4.4 ± 0.3), 31 hummingbird visits (31.4 ± 1.5), and 30 visits by perching birds (29.6 ± 2.5). Number of visits was positively correlated with the number of flowering umbels ($r^2 = 0.7$, $p < 0.05$).

We then conducted a survival analysis by species to which censored data were less than 20% (large sample sizes) and using inflorescence (panicle) height, number of flowering umbels, and distance to closest conspecific as covariates. We found no significant differences among hummingbirds using agaves with either tall or short inflorescences (*A. violiceps*, $\chi^2 = 0.118$, $df. = 1$, $p < 0.7314$; *E. fulgens*, $\chi^2 = 0.315$, $df. = 1$, $p < 0.5749$; *C. pulcher*, $\chi^2 = 0.004$, $df. = 1$, $p < 0.9475$; Fig. 4(b)). In contrast, agaves with the tallest inflorescence were visited sooner by *I. parisorum* ($\chi^2 = 7.213$, $df. = 1$, $p < 0.0072$; Fig. 5(b)) than those with shorter inflorescences. For all cases, no significant differences were observed between survivorship curves using number of panicles (few and many) and distance to closest conspecific (close and far) as covariates ($p > 0.05$).

Foraging modes and pollination

The mode of flower exploitation varied among species. Hummingbirds foraged mostly by hovering along the peripheral flowers and only occasionally clinged or perched on

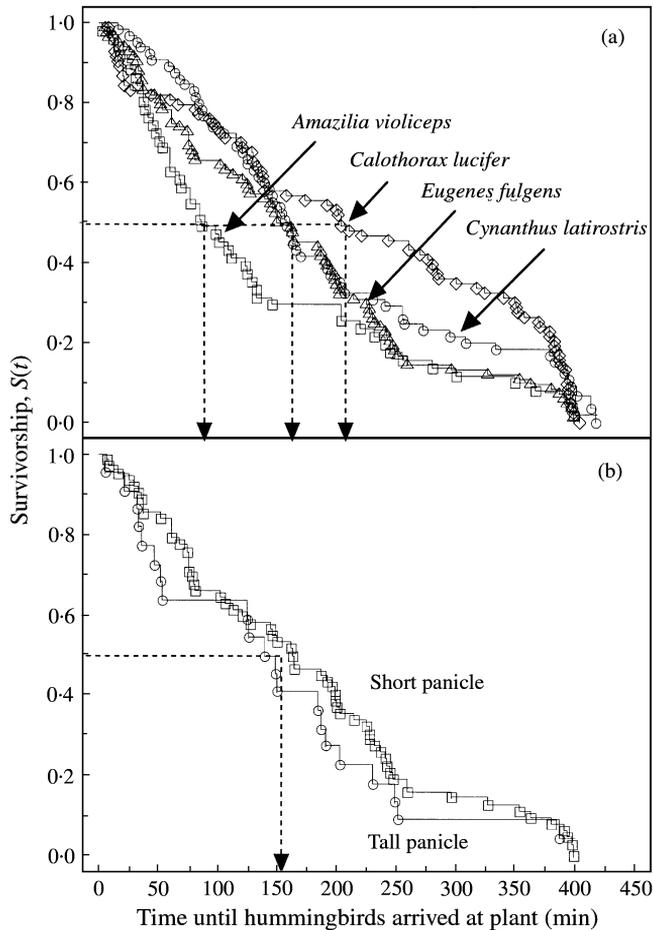


Figure 4. Nonparametric survival functions showing visitation of hummingbirds in *Agave marmorata*. (a) Most frequent species (<20% censored data). (b) By inflorescence height. Note that the probability for agaves with short and tall inflorescences to be visited by hummingbirds is the same.

the perianth of flowers while feeding. Pollen grains were not detected on six hummingbirds mistnetted during our observations. In contrast, orioles foraged by clinging acrobatically to peripheral flowers of umbels (16%), perching on the peduncle of umbels (37%), and mostly sitting on top and center of the umbel (47%). We also observed orioles contacting anthers (becoming dusted with pollen) as they moved from umbels containing mostly staminate flowers (top of inflorescence) to umbels containing both staminate and pistillate flowers (bottom of inflorescence), as they get dusted with pollen. Nocturnal, nectar-feeding bats (*C. mexicana* and *L. nivalis*) used flowers by flying to and instantaneously sitting on the perianth of the peripheral flowers, making no contact with the anthers or stigmas. This type of foraging behavior is unusual among nectar feeding bats. Nectar feeding bats mostly hoove and dip heads in stigmas and anthers, always making stigma contact. Spingid moths visited flowers similar to hummingbirds.

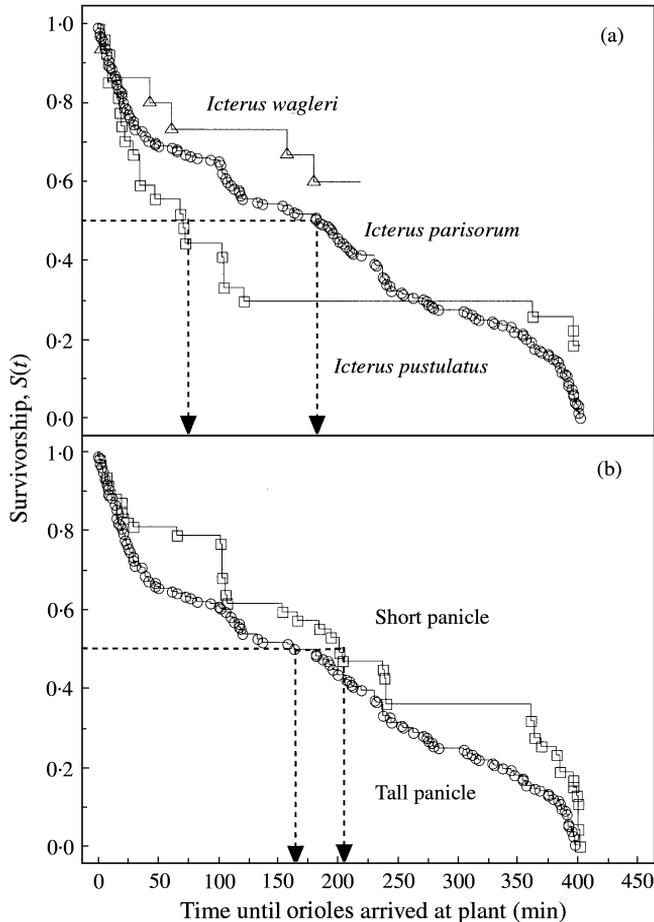


Figure 5. Nonparametric survival functions showing visitation of orioles in *Agave marmorata*. (a) Most frequent orioles. (b) By inflorescence height for *I. parisorum* (<20% censored data). Note that agaves with taller inflorescences are visited sooner by *I. parisorum* orioles.

Discussion

We have shown temporal segregation among nectarivores at *Agave marmorata* (Agavaceae) inflorescences in the Tehuacán Valley, México. Significant differences in survivorship curves were found among *Xylocopa*, hummingbirds, and perching birds. Within assemblages, hummingbirds were temporally segregated. Simple differences in visitation frequency rather than temporal segregation in flower visitation could cause differences in survivorship among hummingbird species. If so, the most frequent visitor would have a much steeper survivorship curve. This was not the case for hummingbirds since the most common visitors (*E. fulgens* and *C. pulcher*) did not show the steepest survivorship curves (Fig. 4). We propose that temporal segregation among hummingbirds be determined by differences in size, where small hummingbirds use agaves later than larger species. This segregation strategy may allow small hummingbirds such as *C. pulcher* to reduce the risk of injury during encounters with more aggressive, territorial hummingbirds such as *A. violiceps*. In contrast, orioles seem to be temporally and spatially segregated depending on the size of the agave

Table 1. Number of bird visits and characteristics of *Agave marmorata* plants

Plant	Panicle height (m)	Number of flowering umbels	Distance to closest flowering conspecific (m)	Number of <i>Xylocopa</i> visits	Number of hummingbird visits	Number of perching bird visits
1	5.42	11	12.5	3	29	29
2	4.10	8	6.3	4	30	7
3	6.20	13	7.0	3	32	93
4	5.40	14	7.0	2	10	19
5	4.95	9	6.3	7	52	15
6	3.30	7	9.3	1	9	7
7	6.60	13	17.1	1	55	50
8	6.15	15	99.0	10	45	16
9	6.65	9	8.9	9	40	53
10	8.35	11	8.9	4	12	7

inflorescence. Temporal and spatial segregation are indicated by the subtle differences in the shapes of survivorship curves—plateaus indicating periods of low visitation, and steep segments indicating periods of high visitation (Fig. 5). This result must be taken with caution because of small sample sizes.

Temporal and spatial segregation vs. territoriality

Behavioral dominance has been proposed as the mechanism by which communities of nectarivores are structured. We believe that the observed patterns of temporal segregation indicate that direct interference among taxa is not the only way to access nectar resources in the agave system, as previously suggested by Martínez del Río & Eguiarte (1987). In fact, we observed that most of the aggressive encounters and chases were among conspecifics.

Temporal segregation may allow floral visitors to reduce inter-specific interactions relative to intra-specific interactions and, therefore, facilitate coexistence. Access to nectar resources by species-mixed assemblages is often determined by inter-specific aggression in which larger species dominate the smaller ones (Ford & Paton, 1982). During our observations, inter-specific chases were rarely observed. Most commonly, intra-specific aggressive encounters were observed among species of orioles and hummingbirds. Because territories are so closely tied to nectar resources, territorial species may play a major role in determining the overall composition and structure of hummingbird assemblages (Wolf *et al.*, 1976; Feinsinger, 1976; Carpenter, 1978; Des Granges, 1978). In this sense, *Amazilia violiceps* aggressively excluded other smaller species (*C. latirostris*, *C. sordidus*, and *C. pulcher*) from agaves. It is believed that the losers of these interactions would use dispersed, low-reward flowers and/or adopt opportunistic behaviors (i.e. traplining) to obtain nectar from aggressively defended patches of nectar (e.g. Feinsinger, 1976; Carpenter, 1978). The assumption that interspecific competition occurring in our system is wholly unsupported by our data, so 'co-existence' may not even be a problem of interest within this assemblage of nectarivores. That is, we have no evidence that population growth of any of the nectarivores in this study is limited by *A. marmorata* nectar, but they certainly rely on this agave to meet their short-term energy requirements. At best, our data suggest that

one alternative and efficient way to avoid aggressiveness from territorial species and to have access to the only existing nectar source is to segregate temporally (i.e. hummingbirds).

There is some evidence of competitive interactions between nectarivorous birds and insects (Schluter, 1986). Schluter (1986) suggested that the bees influence nectar use by the birds and that character displacement in bird body size occurs in response to the presence or absence of bees. It has been observed a size-dependent dominance hierarchy exists among several groups of birds and insects (Brown *et al.*, 1978; Gill & Wolf, 1979; Schaffer *et al.*, 1979; McFarland, 1986; Martínez del Río & Eguiarte, 1987), where birds have negative effects on the availability of nectar to the insects (Lyon & Chadek, 1971; Primack & Howe, 1975; Boyden, 1978; Carpenter, 1979). On the other hand, insect nectarivores can also swamp the resource-defense systems of birds by sheer force of numbers (Schaffer *et al.*, 1979; Kodric-Brown & Brown, 1979; Gill *et al.*, 1982), as observed for honeybees in our study site. Furthermore, the access to nectar resources by co-occurring species can be often determined by inter-specific aggression in which larger species dominate the smallest species (Brown *et al.*, 1978; Collins, 1985). Body size among diurnal visitors to *A. marmorata* ranged from 30 to 320 mg dry wt. in bees (Schaffer *et al.*, 1979), 2.7 to 8.5 g in hummingbirds (Ornelas, 1995), and 20–45 g in orioles (Stiles & Skutch, 1989). However, the absence of inter-specific aggressive interactions among distantly related taxa in *A. marmorata* suggest that a size-dependent dominance hierarchy cannot be used as a generalization for nectar partitioning in the whole assemblage of nectarivores, as previously suggested (Brown *et al.*, 1978; Martínez del Río & Eguiarte, 1987).

Pollination of agaves by perching birds

Agaves or century plants are pollinated by a variety of animals that range from insects to birds and bats (Shaffer & Schaffer, 1977; Howell, 1979; Schaffer *et al.*, 1979; Howell & Roth, 1981; Gentry, 1982; Sutherland, 1987; Kuban, 1989; Slauson, 2000; Arizaga *et al.*, 2000). Many paniculate agaves have morphological, biochemical, and phenological traits that are consistent with the syndrome of chiropterophily (Faegri & Van der Pijl, 1971; Howell & Roth, 1981; Sutherland, 1987; Slauson, 2000; Arizaga *et al.*, 2000). These characteristics include flowers with large floral tubes that are presented in clusters on tall candelabro-shaped inflorescences, copious quantities of nocturnally produced nectar and pollen, pale yellow to bright-yellow flowers, and a floral scent similar to fermenting or rotting fruit (Slauson, 2000). However, several species of agaves presumably pollinated by bats are also heavily visited by bees, hummingbirds, and perching birds through the course of a day (Howell, 1979; Schaffer *et al.*, 1979; Cruden *et al.*, 1983; Kuban *et al.*, 1983; Martínez del Río & Eguiarte, 1987; Sutherland, 1987; Kuban, 1989; Slauson, 2000; Arizaga *et al.*, 2000, this study).

Slauson (2000) showed that bats are not important pollinators of *A. chrysantha* Peebles, but *A. palmeri* possessed floral characteristics for multiple diurnal and nocturnal pollinators. She suggested that some paniculate agaves have a more diurnal, generalist pollinator strategy. Our behavioral observations suggest that bees, sphingids, hummingbirds, and bats were acting as pollen and nectar thieves since they hardly touched the reproductive organs of *A. marmorata*. The possibility that bats are acting as nectar thieves in agaves deserves future detailed studies on their foraging behavior. In contrast, orioles and other perching birds may be acting as pollinators of *A. marmorata* since pollen is easily adhered to the ventral parts whereas foraging on the top of an umbel. This behavior has been previously observed in *A. salmiana* Otto ex Salm (Martínez del Río & Eguiarte, 1987), but the role of perching birds as

pollinators was not evaluated. Kuban (1989) found doves and orioles to be major pollinators on *Agave havardiana*. Of interest to our study is that we found birds to be important pollinators well within the range of nectar feeding bats, while Kuban's work was done in Texas where bats may be more unreliable visitors. Our study also suggests that some tropical species, such as *Agave marmorata*, are not so dependent on bats.

Given the complex nature of segregation processes among distantly or closely related species, the segregation patterns described here can be explained considering the short-term energy requirements of hummingbirds. If animals do in fact segregate due to resource limitation, the effects of such segregation on plant reproductive success would then depend on (1) the timing of agave pollen dehiscence and stigma receptivity, (2) how pollen transfer is achieved within and among plants, and (3) the role floral visitors play as pollinators. Kuban (1989) and Slauson (2000) have proposed that adaptations that arose as a result of bat pollination has pre-adapted many agaves to a multiple vertebrate pollinator syndrome, and that these floral characters have been so effective that only minor changes in the agave 'bat pollination syndrome' has occurred. Our results suggest that in *Agave marmorata* also minor shifts in floral characteristics have evolved to attract diurnal pollinators where bats are not longer reliable pollinators (i.e. nectar thieves). These floral characters include the large amounts of pollen closer to dawn, diurnal nectar production, diurnal pistil receptivity, and bright yellow flower color. Although we do not know which species is the most effective pollinator, our behavioral data suggest that orioles are the most likely candidates. Westerkamp (1990) listed some of the characteristics of blossoms adapted to perching birds, including (1) inflorescences composed of a large number of flowers, (2) most flowers in anthesis at any given time, (3) visitors reach several flowers from a single perch without considerable additional movement, (4) inflorescences must be strong enough for the bird to land on, and (5) flowers must be of a strong fabric. Besides this, we believe that the horizontal bending of anthers, as orioles land on the umbel, is an unnoticed floral trait that facilitates pollen adhesion to the ventral area of perching birds.

Species diversity of agaves is highest in the mesic habitats of Central Mexico (Gómez-Pompa, 1963) where the evolution of inflorescence and floral characters in paniculate agaves may have been influenced by bat pollination (Howell, 1979; Gentry, 1982). However, many species have successfully radiated into more arid environments of central and northern Mexico and southwestern United States, which are beyond or near the edges of the range of nectarivorous bats (Slauson, 2000). Results of this study and those of Kuban (1989) and Slauson (2000) suggest that several species of paniculate agaves have evolved minor shifts in floral characteristics that may promote a multiple or generalist pollination syndrome. Floral shifts observed in *A. marmorata* (pollen, and nectar production, stigma receptivity) may also serve as possible adaptations that increase diurnal pollination. A phylogenetic approach would help us to elucidate (1) the origin of bird and bat pollination among paniculate agaves, (2) the lack of pollinator specialization in agaves distributed in environments with variable climatic conditions, as proposed by Slauson (2000), and (3) morphological and physiological floral traits correlated accordingly to shifts in pollinator type.

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