

AMERICAN JOURNAL OF Botany

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Author(s): Carlos N. Ibarra-Cerdeña, Luis I. Iñiguez-Dávalos and Víctor Sánchez-Cordero

Source: *American Journal of Botany*, Vol. 92, No. 3 (Mar., 2005), pp. 503-509

Published by: [Botanical Society of America](#)

Stable URL: <http://www.jstor.org/stable/4123899>

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**POLLINATION ECOLOGY
OF *STENOCEREUS QUERETAROENSIS* (CACTACEAE),
A CHIROPTEROPHILOUS COLUMNAR CACTUS, IN A
TROPICAL DRY FOREST OF MEXICO¹**

CARLOS N. IBARRA-CERDEÑA,² LUIS I. IÑIGUEZ-DÁVALOS,^{3,4} AND
VÍCTOR SÁNCHEZ-CORDERO²

²Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70-153, 04510, Mexico, D. F., Mexico; and ³Instituto Manantlán de Ecología y Conservación de la Biodiversidad, Universidad de Guadalajara, Av. Independencia Nacional 151, 48900, Autlán, Jalisco, Mexico

Flowers of columnar cacti are animal-pollinated, often displaying a chiropterophilic syndrome. This study examined if the columnar cactus *Stenocereus queretaroensis*, a tropical species endemic to western Mexico, is bat-pollinated, by studying its pollination biology and the foraging behavior of potential pollinators. Flowers were produced in winter through spring, peaking in April. Anthesis was nocturnal, and stigma and anther turgidity began around 2200 hours. Production of nectar secretion and highest sugar concentration and energy supply were nocturnal, peaking between 2200 and 2400 hours. Manual auto-pollination and exclusion experiments showed that self-pollination yielded no fruits, while nocturnal pollinators resulted in high fruit set and seed set compared to diurnal pollination treatments. The nectar-feeding bat *Leptonycteris curasoae* (Phyllostomidae) was the main nocturnal pollinator with the highest effective pollination. Peak bat visitation coincided with peaks in nectar production. The high abundance of *L. curasoae* throughout the 4-yr study, suggests that it is a seasonally reliable pollinator for this columnar cactus. While pollination syndromes have been increasingly called into question in recent years, this study suggests that at least for this system, there is a fairly close fit between pollinator and pollination syndrome.

Key words: Cactaceae; columnar cacti; *Leptonycteris curasoae*; mutualism; nectar-feeding bat; pollination ecology; *Stenocereus queretaroensis*; west central Mexico.

Stebbins (1970) proposed that the evolution of pollination systems in animal-pollinated plants has been driven by the foraging behavior of the main pollinator, regardless of other pollinator visits to a particular plant. This “most effective pollinator principle” (sensu Stebbins, 1970) implies selection on floral phenotypes that match morphology of the most effective pollinators. Specialized pollination systems are those that attract a limited subset of potential pollinators, often of a particular taxonomic group (e.g., long-tongued hawkmoths, bees, hummingbirds, bats), and the flowers reflect the size, morphology, and behavioral traits of the pollinators (Baker, 1961; Faegri and van der Pijl, 1979). Conversely, empirical evidence suggests that pollination mutualisms often are diversified and opportunistic (Waser et al., 1996; Olesen and Jordano, 2002), having different levels of generalization, in part reflecting temporal and spatial fluctuation in the local abundance of polli-

nators (Waser et al., 1996). In most plant species, a wide array of taxonomically diverse fauna such as insects, birds, and mammals usually serve as potential pollinators (Ollerton, 1996; Aigner, 2001).

Based on flower morphology and nocturnal anthesis, Valiente-Banuet et al. (1996) proposed that most of the Pachycereae tribe is bat-pollinated, a prediction that has been widely supported (Fleming et al., 1996; Sahley, 1996; Nassar et al., 1997; Valiente-Banuet et al., 1997a, b; Casas et al., 1999; Molina-Freaner et al., 2004). However, in some of these cactus species, bats are not the exclusive pollinators, and other groups such as some birds or insects can act as the primary pollinators (Alcorn et al., 1959; McGregor et al., 1962; Fleming et al., 1996, 2001; Sahley, 2001; Molina-Freaner et al., 2004). Pollination systems appear to vary along a latitudinal gradient, ranging from tropical specialization to temperate generalization (Olesen and Jordano, 2002, but see Ollerton and Cranmer, 2002). Such a pattern has been identified in paniculate agaves, a group of plants that interact with nectar feeding-bats in North America (Arizaga et al., 2000; Slauson, 2000; Molina-Freaner and Eguiarte, 2003). Similarly, chiropterophilic columnar cacti seem to vary latitudinally in their reliance on different pollinators (Valiente-Banuet et al., 1996; Fleming et al., 2001). Extratropical chiropterophilic cacti appear to be faced with unpredictable seasonal year-to-year variation in pollinators, and thus plants tend to have a generalist pollination system (Sahley, 1996, 2001; Fleming et al., 2001). Conversely, cacti in tropical regions have a specialized pollination system because of the highly reliable seasonal availability of nectar-feeding bats, thereby leading to a temporally stable pollination system (Petit, 1995; Nassar et al., 1997; Valiente-Banuet et al., 1997a, b; Casas et al., 1999).

¹ Manuscript received 2 April 2004; revision accepted 18 November 2004.

Helpful comments on earlier versions of the manuscript were provided by A. Casas, E. de la Barrera, L. Eguiarte, A. Valiente-Banuet, and E. Yezpez. We thank N. Holland and an anonymous reviewer for critical comments that greatly improved the manuscript. I. Cuadriello helped in identifying the insects. We especially thank the Villaseñor family for allowing us to conduct field work on their land, and C. Gómez, P. Ibarra, H. Munguía, H. Orozco, I. Ruan, G. Tinoco, A. Rodríguez, C. Roy, D. Zamora, and D. Villaseñor for assistance in the field and in the lab. The authors wish to thank the Instituto Manantlán de Ecología y Conservación de la Biodiversidad of the Universidad de Guadalajara, and the Instituto de Biología of the Universidad Nacional Autónoma de México for logistical and financial support. This work was partially supported by grants from the North American Bat Conservation Partnership (NABCP) to LIID, and Bat Conservation International (BCI) with a student scholarship fellow to CNIC. The Red Latinoamericana de Botánica awarded CNIC with a graduate scholarship (RLB-03-M1).

⁴ Author for reprint requests (e-mail: liniguez@cucsur.udg.mx).

Two columnar cacti, *Stenocereus queretaroensis* (Weber) Buxbaum and *Pachycereus pecten-aboriginum*, coexist in tropical dry forests in the State of Jalisco, in west-central Mexico. Both cacti partially overlap in their reproductive season. *Stenocereus queretaroensis* and *P. pecten-aboriginum* have nocturnal anthesis with a chiropterophylic syndrome, although flowers remain open until the afternoon of the following day. *Pachycereus pecten-aboriginum* did not produce flowers in 2002 and 2003, and *S. queretaroensis* was the main food source for pollinators during that period (Ibarra-Cerdeña et al., unpublished data). The pollination system in *S. queretaroensis* appears to be chiropterophylic, although several animals forage on its flowers (CNIC and LIID, personal observations). This apparent paradox of flowers with specialization having a complex community of floral visitors (Ollerton, 1996) should be resolved by showing that only a small proportion of the visitors' assemblage act as effective pollinators (Johnson and Steiner, 2000). This has been demonstrated in *Calathea ovan-densis* (Schemske and Horvits, 1984), where a diverse assemblage of insects visit flowers, but only a small proportion of species acts as effective pollinators.

In this study, we propose that nectar-feeding bats are the main pollinators (sensu Stebbins, 1970) of *S. queretaroensis* in Jalisco among a diverse assemblage of potential pollinators in this region. We predicted a strong correlation between nectar production and foraging behavior of nectar-feeding bats. Further, because *S. queretaroensis* produces flowers every year, this cactus can be considered a reliable food source for the nectar-feeding bat that seasonally visit their populations, and we predicted that bat abundance among years should be constant rather highly variable.

MATERIALS AND METHODS

Study area—This study was conducted in *S. queretaroensis* stands around the city of Autlán, in the Autlán valley in the state of Jalisco, west central Mexico. This area is located between the 19°42'44" N and 19°53'52" N and the 104°14'10" W and 104°25'38" W. Elevation is around 900 m a.s.l. Average annual temperature ranges from 20°C to 28°C, and annual precipitation ranges from 600 mm to 1000 mm. Vegetation varies from thorn-scrub and tropical deciduous forest in the valley and lower dry slopes to oak and oak-pine forests at higher altitudes.

Study species—*Stenocereus queretaroensis* is an arborescent columnar cactus up to heights of 10 m with a short trunk and numerous vertical stems. The cylindrical stems generally have eight prominent ribs and a diameter of 13 to 18 cm. Flowers are 10 to 14 cm long and grow from areolas along the upper half of branches (Pimienta-Barrios and Nobel, 1994). In the Autlán Valley, this cactus typically reaches sexual maturity at a height of 3 m, with a trunk diameter of 12 cm or a canopy diameter greater than 1.5 m (Benz et al., 1997). *Stenocereus queretaroensis* is endemic to western central Mexico and widely distributed in the semiarid regions of Jalisco, Colima, Guanajuato, Michoacan, Queretaro, and Zacatecas (Pimienta-Barrios and Nobel, 1994).

Floral phenology—Flower phenology was studied by counting all flowers produced by the same 25 mature plants every week during the blooming season in February 2002 and 2003, until no plants were found with buds or flowers, in mid-June. In both years, after the blooming period, we visited the *S. queretaroensis* stands once a month to check for flowers at other times of the year. Mean flower production per individual was calculated by integrating the area under the phenology curve for the 2002 and 2003 reproductive season.

Floral biology—To characterize the flowers, one flower was collected from 12 individuals and preserved in a solution of formalin, acetic acid, and 70%

ethanol (FAA, 5 : 5 : 90 v/v). Floral size was determined by measuring external and internal flower length, perianth width, distance of anthers and stigma to base of floral tube (Nassar et al., 1997). Hermaphrodite flowers were verified by checking ovules in ovaries and pollen in anthers in this sample. Ovules of each ovary were counted and used for the seed set analysis. The times of anthesis and flower closing were recorded for a randomly chosen flower on each of 10 plants. Flower receptivity was evaluated at the same time by observing anthers and stigma turgidity every hour from opening until closure. Nectar production was measured by removing nectar with a 1-mL graduated syringe every 2 h from one bagged flower per plant ($N = 11$) from 2000 hours until 0800 hours next morning; this hour was chosen because we sampled some flowers for an entire morning during 2002 and no nectar was produced after that hour (Ibarra-Cerdeña et al., unpublished data). Sugar concentration was quantified using a hand-held refractometer (BRX30 No 137530LO, Leica, USA) with automatic temperature compensation. Refractometer data were interpreted as sucrose percentage (Dafni, 1992). Energy supply was calculated as $J = 16.8[(S/100) VD]$, where J is the energy expressed in joules, S is a percentage of sugar reading in the refractometer, V is nectar volume in μL , and D is density of sucrose at the observed concentration (see table 6 in Dafni, 1992).

Pollination system—To examine self compatibility and contributions of nocturnal and diurnal pollinators in fruit set and seed set, we conducted five treatments for pollination experiments on 130 marked flowers on 75 plants: (1) natural self-pollination (30 flowers of 15 plants)—buds were bagged with mosquito netting and left until flower closure; (2) manual self-pollination (30 flowers on 15 plants)—buds were bagged and later hand pollinated with their own pollen 2 or 3 h after anthesis (when stigma turgidity was higher), and rebagged until flower closure; (3) nocturnal pollination (20 flowers on 15 plants)—flowers were left exposed to pollination visits throughout the night, then bagged just before 0500 hours when nocturnal visitors ceased activity and diurnal pollinators were not yet active; (4) diurnal pollination (20 flowers on 15 plants)—buds were bagged during the night with mosquito netting and bags were removed at 0600 hours when no nocturnal pollinators were observed and diurnal pollinators began to forage on flowers; and (5) open pollination (30 flowers on 15 plants)—flowers were labeled and left unbagged, and thereby available to both nocturnal and diurnal pollinators. All the experiments were conducted on four consecutive days in 2003, except the manual self-pollination, which was done in 2004. For each of the five treatments, we recorded whether flowers aborted or produced mature fruit. Mature fruits were collected for seed counting 4 wk after the experiments. Because we were not able to recover all fruits from the experiments as a result of harvesting by local people, seed set was analyzed for 17 control fruits and seven fruits each for nocturnal and diurnal pollination treatments. To estimate the efficiency of pollinators, we calculated the seed set (seed produced by fruit/average number of ovules) for each treatment.

Floral visitors—Diversity, abundance, and activity of night visitors were recorded using a Sony Digital Handy cam DCR-TRV740 with a night-shot feature. The camera was placed 1 to 1.5 m below flowers using a small tripod tied to the stem. This provided a clear shot of the anthers and stigma, plus space to record the entire bat. Videotaping began at sunset before anthesis and continued until 0500 hours because the activity of nocturnal visitors always stops before that hour. For each flower visited, we recorded species, duration of visit, and if visits were legitimate (i.e., visitor's body came in contact with anthers and/or stigma), or illegitimate (no contact with anthers or stigma), regardless of the harvesting of nectar that the visitor can or cannot do. Insects were identified to family and bats to species based on morphological characters and size.

To estimate the abundance of nectar-feeding bats, we captured bats once a week with mist nets in four consecutive years (2000–2003), using 12 m wide and 3 m high mist nets, which were placed inside and near cacti patches, throughout the cactus reproductive season. In 2000, two mist nets were used, generally open from 0800 to 0200 hours (46 net-h in 4 wk); in 2001, three mist nets were used, generally open from 0800 to 0500 hours (210 net-h in 8 wk); in 2002, three mist nets were open generally from 0800 to 0500 hours

(195 net-h in 8 wk); and in 2003, three mist nets were opened generally from 0800 to 0500 hours (170 net-h in 7 wk).

We used binoculars to visually observe diurnal visitors on focal flowers during 9 d in May 2002. Observation lasted for 10 min at 30-min intervals from 0730 until 1040 hours, observing four nearby flowers each day. The total observation time was 360 min (6 h). We recorded the visitor's species, and, in the case of birds, we counted the number of visits. Some insects were collected to identify the species.

Statistical analysis—We performed a goodness of fit analysis to test if frequencies in fruit or abort result in pollination experiments (nocturnal and diurnal pollination) deviated significantly from the control experiment, which was used as the expected frequency. The effect of pollinator exclusion on seed set was analyzed using a Kruskal-Wallis test, with SPSS 10.0 software (SPSS Inc., Chicago, Illinois, USA). Due to the curvilinear response over time of nectar volume, nectar concentration and energy supply, these data sets were analyzed with a second-order polynomial regression (Neter et al., 1996) using JMP 4.0.2.n (SAS Institute Inc., Cary, North Carolina, USA).

RESULTS

Floral phenology—In 2002, the flowering season began relatively early; when we did the first sample, the average number of flowers per individual was 5.3; the peak occurred in mid-March (11.25 flowers per individual per day) and ended in mid-April. The reproductive season of 2003 began with bud production of *S. queretaroensis* in early February, although the flowers were present by late February. Flower production peaked in mid-April (4.7 flowers per individual per day) and extended through early June (Fig. 1). Mean of flowers produced in the season by each individual was 322.18 in 2002 and 192.6 in 2003.

Floral biology—The *S. queretaroensis* flowers ($N = 12$ plants) had a total length of 88.77 ± 0.61 mm; the internal length was 70 ± 5.46 mm; perianth width was 48 ± 1.20 mm. The stigma length measured 70.03 ± 1.58 mm and the anthers 58.85 ± 1.02 . All the flowers were hermaphrodites. During the flowering season, flowers started to open at 1940 ± 0.13 hours ($N = 10$ plants) and closed at 1530 ± 0.2 hours. Maximum elongation of anthers, turgidity of stigma, and retraction of tepals were observed at 2200 ± 0.1 hours ($N = 10$ plants); this condition was maintained throughout the night until next morning, when they were flaccid.

Nectar secretion at anthesis was 0.16 ± 0.04 mL and rapidly peaked at midnight (0.37 ± 0.03 mL) (4 h after anthesis), gradually decreasing until 0800 h when virtually nothing remained (0.03 ± 0.01 mL) ($R^2 = 0.47$, $F = 28.03$, $P < 0.0001$, $N = 11$; Fig. 3a). Sugar concentration was relatively high (20.17 ± 0.5) at anthesis (2000 h), peaking 2 h later (21.37 ± 0.43) and steadily decreasing towards 0800 hours (9.54 ± 3.04) ($R^2 = 0.62$, $F = 51.3$, $P < 0.0001$, $N = 11$; Fig. 3b). The amount of energy offered by flowers peaked between 2 h and 6 h after anthesis and reached a maximum at 2400 hours (13.90 ± 1.15 J), maintaining maximum energy availability for only 4 h ($R^2 = 0.47$, $F = 28.03$, $P < 0.0001$, $N = 11$; Fig. 3c).

Pollination system—Fruits were not produced by self-pollination treatments, either natural or manual. Control, diurnal and nocturnal treatments produced ripe fruits after approximately 32 d. Fruit set was 0.93 in control, 0.87 in nocturnal, and 0.4 in diurnal pollination treatments; no difference was found between nocturnal and open pollination ($\chi^2 = 1.071$, df

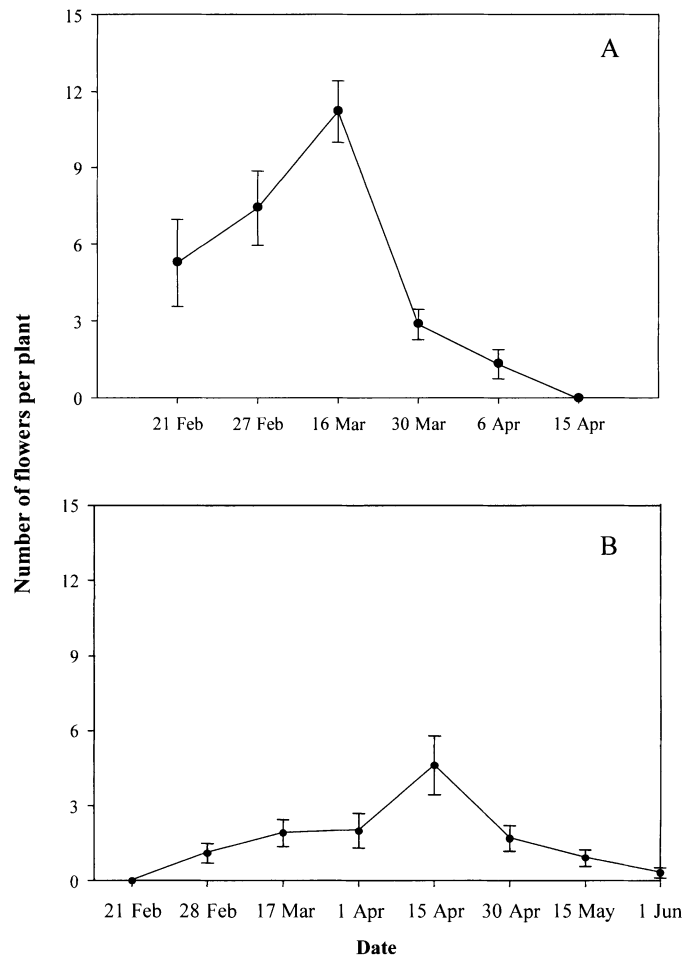


Fig. 1. Flower phenology (mean flowers per day per plant ± 1 SE) of *Stenocereus queretaroensis* in (A) 2002 and (B) 2003 ($N = 25$ plants).

= 1, $P > 0.1$), as in the diurnal pollination treatment ($\chi^2 = 68.57$, df = 1, $P < 0.001$; Table 1). Statistical differences were observed in seed set between open (mean = 922.88 ± 49.75 SE), nocturnal (mean = 943.57 ± 84.82) and diurnal pollination treatments (mean = 207 ± 58.31) producing less seeds in the last treatment ($\chi^2 = 15.78$, df = 2, $N = 31$, $P < 0.0005$).

Flower visitors—Most nocturnal visits to flowers occurred near midnight. Only two species of nocturnal flower visitors were observed in 65 h of videotaping of 10 focal flowers throughout the reproductive season of *S. queretaroensis* (Fig. 3). At least one undetermined hawkmoth species (Sphingidae) was observed visiting flowers at midnight (28 records), but all the visits were illegitimate; hawkmoths touched neither stigmas nor anthers when robbing nectar with their long probosces (the body was always at least 4 cm above the anthers and stigma). The nectar-feeding bat *Leptonycteris curasoae* (Glossophaginae, Phyllostomidae) was the most frequent flower visitor (187 records) and the only bat species observed (Fig. 3a). Ninety-five percent of all bat visits were males; we were not able to determine the sex of the other 5%. Bats had two feeding behaviors—illegitimate (maybe exploratory visits) when bats flew over without touching flowers (42 records), and legitimate, when bats consumed nectar or pollen touching the

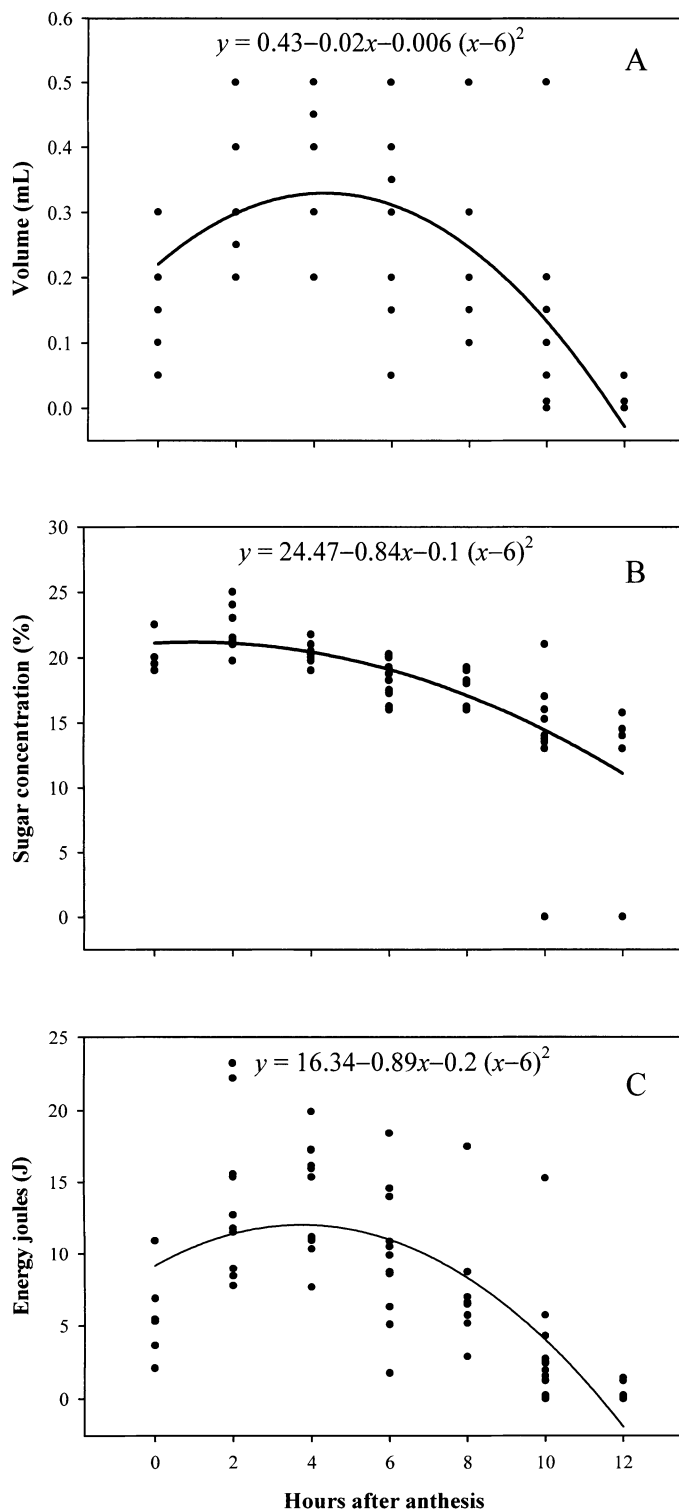


Fig. 2. (A) Nectar production during anthesis ($N = 11$ flowers), (B) nectar quality measured as percentage concentration, and (C) energy supply of nectar in *Stenocereus queretaroensis* flowers, quantified every 2 h starting with anthesis.

stigma or anthers, by introducing the head and neck inside the floral cavity (145 records). Of the legitimate bat visits, 93.8% (136 records) were for nectar consumption and all resulted in pollen hair-adherence or pollen deposit in stigma surface. The

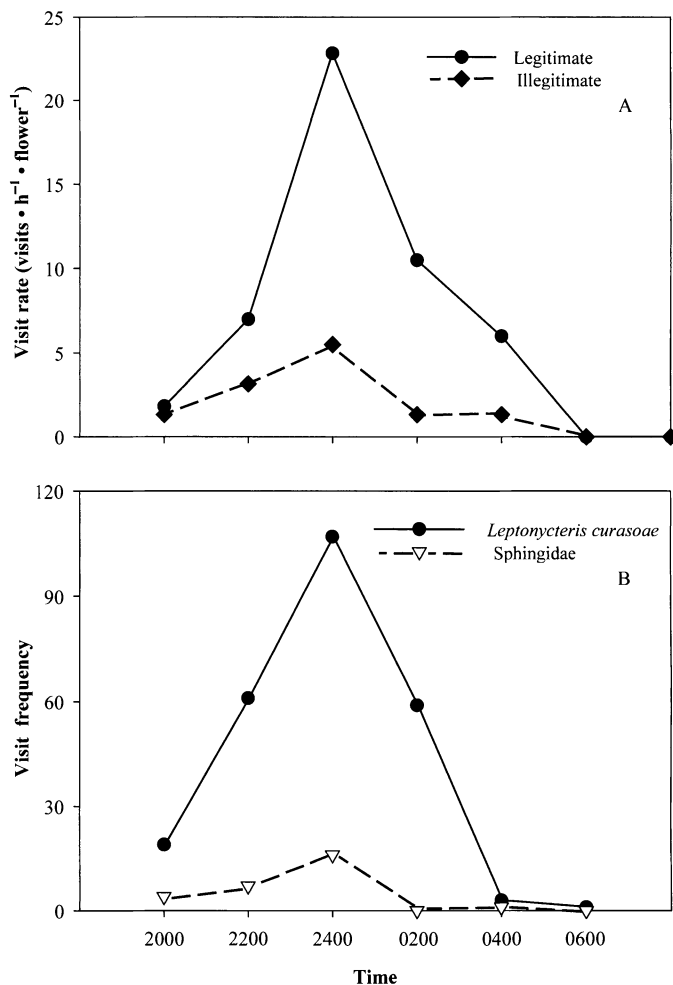


Fig. 3. Nocturnal visits to selected flowers of *Stenocereus queretaroensis* in Mexico during the reproductive season. (A) Legitimate and illegitimate visit of the nectar-feeding bat *Leptonycteris curasoae* in flowers of *S. queretaroensis*, and (B) frequency of visits of an undetermined hawkmoth in comparison to those of *L. curasoae*.

remaining 6.2% (9 records) of legitimate visits were for pollen consumption (the bat flew over the flower and bit the anthers), and the stigma was always touched (either with the forefront or the throat, depending on the arrival direction). Both hawkmoth and bat visits peaked at 2400 hours; legitimate and illegitimate visits showed similar timing, although illegitimate visits were fewer (Fig. 3b). *Leptonycteris curasoae* was the most frequently captured bat in four consecutive years, although capture rate differed between years. Other species of nectar-feeding bats (*Glossophaga soricina* and *Choeronycteris mexicana*) were rare (Table 2).

Regarding diurnal visitors, we recorded four bird species with legitimate visits to the flowers, two hummingbirds, *Amazilia beryllina* (41 records) and *Cyananthus latirostris* (20 records), the woodpecker *Melanerpes chrysogenis* (8 records) and the oriole *Icterus pustulatus* (5 records). Visitation rate of birds was considerably low compared with the nocturnal visitors. Visit rate was higher early in the morning and decreased after 0900 hours. The hummingbird *A. beryllina* had the highest visit rate followed by *C. latirostris* and next by the oriole *I. pustulatus* and the woodpecker *M. chrysogenis* (Fig. 4).

The insects recorded were mainly honey bees (*Apis melli-*

TABLE 1. Fruit set (fruits/flowers), seeds produced, and seed set (number of seeds per fruit/ovules, mean of 12 flowers) in open, nocturnal, and diurnal treatments.

Treatment	Fruit set		Seeds produced		Seed set		Statistical differences
	N (plants)	Fruit set value	N (fruits)	Average number of seeds	Seed set value	SE	
Control (open pollination)	15	0.93	17	922.88	0.73	0.04	A
Nocturnal pollination	15	0.87	7	943.57	0.74	0.07	A
Diurnal pollination	15	0.4	7	207.00	0.16	0.05	B
Natural self-pollination	15	0.0	—	—	—	—	—
Manual self-pollination	15	0.0	—	—	—	—	—

Note: Different letters indicate statistical differences among treatments ($P < 0.0005$).

fera: Apidae), *Epicharis* sp. (Apidae), *Xilocopa* sp. (Apidae), *Exomalopsis* sp. (Apidae), *Lasioglossum* sp. (Halictidae), and *Agoposternon* sp. (Halictidae). Because of the high number of insects, we were not able to determinate their abundance. Typically, the insects remained more than 5 min on one flower to harvest pollen and then flew to other flowers on the same stem.

DISCUSSION

The pollination system in *S. queretaroensis* supports the hypothesis of Valiente-Banuet et al. (1996) that most Pachycereeae cacti are bat-pollinated (but see Fleming et al., 2001). Flower characteristics such as time of flower opening, stigma receptivity period, and nectar production, support a chiropterophylic syndrome in *S. queretaroensis*. These traits in floral biology of *S. queretaroensis* can be associated with the foraging behavior of *L. curasoae*, the main pollinator in our study site.

Reproduction by *S. queretaroensis* occurs only once a year during the dry season. The unimodal pattern of flower production has been described for another locality about 100 km NE of our site (Pimienta-Barrios et al., 2000). The unimodal pattern has been reported also for columnar cacti in subtropical regions of the Sonoran Desert (Fleming et al., 2001); however, in the State of Guanajuato, in central México, there are two flowering periods, one coincides with dry season and other with the fall, at the end of the rainy season (Castillo, 2003).

Cacti grow during the rainy season and stop growing at the beginning of the dry season. Flower display is directly related to the amount of rain in the previous year season (Nobel and Pimienta-Barrios, 1995). We observed variation between 2 yr at the onset of the flowering season, duration of blooming period, and flower production per plant. In another columnar cacti species at our study site, *Pachycereus pecten-aboriginum*, the pattern was similar (Ibarra-Cerdeña et al., unpublished data). This suggests that both columnar cacti are responding to the same factors influencing flower production. Fleming et al. (2001) observed that phenological patterns in cacti of the Sonoran desert are affected by variations in temperature and

precipitation. Although these authors predicted that species with specialized pollination systems must produce a relatively constant number of flowers compared with species having a generalist pollination system, neither their data nor ours support this prediction.

Nectar production was unimodal with an abrupt increase and rapid decrease, reaching the maximum of food supply for nocturnal pollinators around midnight (Fig. 2). Bat visits were observed only when cactus flowers had more than 0.86 mL of nectar, suggesting a threshold for visitation by *L. curasoae* (Horner et al., 1998). Although most columnar cacti produced high amounts of nectar at night, peaks in nectar quantity and quality varied according to species. Most columnar cacti offer high rewards to pollinators a few hours after anthesis, when nectar-feeding bats are more active (Petit and Freeman, 1997; Fleming et al., 1996; Nassar et al., 1997; Molina-Freaner et al., 2004). *Stenocereus stellatus* peaked in nectar production around 0300 hours (Casas et al., 1999), but the timing of visits of pollinators for this cactus is still unknown. Visit rates estimated in Cardon flowers (*Pachycereus pringlei*) peaked around 0200 hours, when flowers had more than 0.8 mL of accumulated nectar (Horner et al., 1998). Given that we did not reinsert nectar, we were unable to determine if nectar removal influenced production, as observed in *Stenocereus griseus* (increasing nectar secretion) or not, as observed in *Subpilocereus repandus* (Petit and Freeman, 1997). Other studies reported no significant or little variation (visits reducing nectar secretion) occurring with simulated visits on nectar production (McDade and Weeks, 2004).

Our study showed that *S. queretaroensis* is incapable of self-pollination, as occurs in other population located in Guanajuato in central Mexico (Castillo, 2003), and with other cactus species (Nassar et al., 1997; Valiente-Banuet et al., 1997a, b; Casas et al., 1999; Molina-Freaner et al., 2004). Both fruit set and seed set were significantly higher in nocturnal than in diurnal treatment, with the nocturnal treatment statistically equal to the open treatment. Fruit set in the open (control) treatment was relatively high compared to studies in the Son-

TABLE 2. Relative frequency of nectar-feeding bats captures in the Autlán Valley during the reproductive season of *Stenocereus queretaroensis* in four consecutive years (2000–2003). The number in parentheses is the number of captured bats.

Species	Frequency of bats* (N)			
	2000	2001	2002	2003
<i>Choeronycteris mexicana</i>	0 (0)	1.4 (3)	1.5 (3)	2 (2)
<i>Glossophaga soricina</i>	2 (1)	1.4 (2)	0 (0)	1.9 (5)
<i>Leptonycteris curasoae</i>	28 (13)	14 (30)	15 (12)	9 (14)
Sampling effort (No. of capture h · net ⁻¹ · night ⁻¹)	46	210	195	170

Note: *Frequency was calculated as (captured individuals · net-h⁻¹ · night⁻¹) × 100.

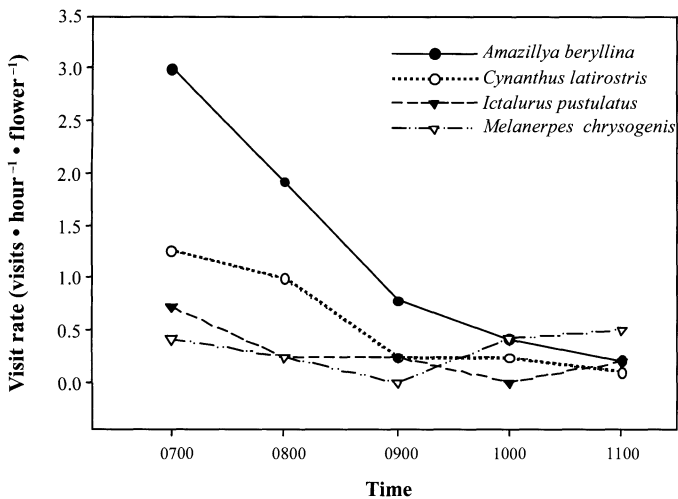


Fig. 4. Visitation rate of birds to *Stenocereus queretaroensis* flowers.

oran Desert, where the nocturnal pollinators are scarcer and variable in abundance (Fleming et al., 2001; Molina-Freaner et al., 2004). However, fruit set reported for tropical species, as in the Tehuacan Valley, Mexico (Valiente-Banuet et al., 1996; Valiente-Banuet et al., 1997a, b; Casas et al., 1999), and Venezuela (Petit, 1995; Nassar et al., 1997) had similar values, suggesting that columnar cacti are not limited by pollinator availability in tropical regions.

Fruit set in *S. queretaroensis* resulted primarily from nocturnal pollination, with values similar to control treatments (Fig. 3b). Nevertheless, diurnal pollinators also contributed to a substantial proportion of fruit set compared with other tropical species (Nassar et al., 1997; Valiente-Banuet et al., 1996, 1997a, b, 2004). It should be noted, however, that their effect on seed production was even lower compared with nocturnal pollinators (Fig. 2); thus nocturnal pollinators were more effective than diurnal at our study site. This might be related to the geographic location, because most tropical columnar cacti depend on nocturnal pollinators, while diurnal or nocturnal pollinators can pollinate subtropical columnar cacti with similar effectiveness (Valiente-Banuet et al., 1996; Fleming et al., 2001). Fleming et al. (2001) argued that the unreliability of *L. curasoae* in the Sonoran Desert is caused by its virtual absence in spring, when flower and bird densities can be high. Although *L. curasoae* density in south central Mexico appears similar to the Sonoran Desert, its reliability as a pollinator in these subtropical regions could be greater because (1) flower density is lower compared with the Sonoran desert cacti, resulting in a high fruit set per bat ratio, and (2) bats are present year-round (Rojas-Martinez et al., 1999).

Visit rates of birds were considerably lower compared with nocturnal visitors. Although flowers remain open until the beginning of the afternoon, the general activity concentrated in the first hours of the morning and decreased in the afternoon, perhaps due to high temperatures and a lack of nectar reward (Fig. 4). We contend that most insects acted as pollen robbers and poor pollinators. *Xilocopa* sp. was perhaps the only exception because these bumblebees spent less time in each flower and flew longer distances; thus they were potentially legitimate pollinators.

Our study showed that hawkmoths acted as nectar robbers, while *L. curasoae* was the only nocturnal pollinator. No other

bats were recorded as visitors. Although the number of captured individuals of *L. curasoae* varied in all four years of bat netting, it was always the most frequently captured species, suggesting that this species is a reliable seasonal pollinator for *S. queretaroensis*, leading to a specialized pollination system (sensu Stebbins, 1970).

Although pollination syndrome models have been challenged recently, with the argument that generalized pollination systems are more frequent than specialized ones and that plants with specialization are pollinated by a broader than expected range of animals (Wasser et al., 1996), our study showed a close association between *L. curasoae* and *S. queretaroensis*, thus suggesting that the chiropterophilic syndrome is still a useful model. Although we recognize the importance of the diurnal pollinators to support a reasonably high fruit production, their relative importance for seed production (seed set) is considerably low. The consequences of the interaction of nectar-feeding bats and columnar cactus are both proximal, because the number of propagules produced by bat pollination is higher than the production of diurnal pollinators, and ultimately, because bat pollination produced greater genetic variability than other pollinators, as shown by Nassar et al. (2003). A remaining challenge is to examine the role of pollinators, seed dispersers, and nurse plants in the population dynamics of the cactus. This has been partially done with the exclusively bat-pollinated cactus *Neobuxbaumia tetetzo* (Godínez-Alvarez et al., 2002). Future research should include the role of several pollinators and dispersers in the population dynamic of *S. queretaroensis*.

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