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COMPARATIVE POLLINATION BIOLOGY OF VENEZUELAN COLUMNAR CACTI AND THE ROLE OF NECTAR-FEEDING BATS IN THEIR SEXUAL REPRODUCTION¹

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The floral biology, reproductive system, and visitation behavior of pollinators of four species of columnar cacti, *Stenocereus griseus*, *Pilosocereus moritzianus*, *Subpilocereus repandus*, and *Subpilocereus horispinus*, were studied in two arid zones in the north of Venezuela. Our results support the hypothesis that Venezuelan species of columnar cacti have evolved toward specialization on bat pollination. Additional information on the floral biology of a fifth species, *Pilosocereus lanuginosus*, was also included. All species showed the typical traits that characterize the pollination syndrome of chiropterophily. All species but *Pilosocereus moritzianus* were obligate outcrossers. Nectar and pollen were restricted to nocturnal floral visitors. Two species of nectar-feeding bats, *Leptonycteris curasoae* Miller and *Glossophaga longirostris* Miller, were responsible for practically all the fruit set in these cacti. Frequency of bat visitation per flower per night was highly variable within and between species of cactus, with average frequencies varying between 27 and 78 visits · flower⁻¹ · night⁻¹. In general terms, the pattern of floral visitation through the night was significantly correlated with the pattern of nectar production and nectar sugar concentration for all species of cactus. Under natural pollination, fruit:flower ratios varied from 0.46 in *Subpilocereus repandus* to 0.76 in *Stenocereus griseus*. The efficiency of bat pollination in terms of seed:ovule ratio was high in all species, varying between 0.70 and 0.94.

Key words: bat; breeding system; Cactaceae; chiropterophily; columnar cactus; Glossophaginae; pollination; Venezuela.

Although many species of columnar cacti are presumed to be pollinated by bats based on their floral characteristics (Valiente-Banuet et al., 1996), little is known about their reproductive biology and pollination ecology. Early studies of the pollination biology of saguaro (*Carnegiea gigantea*) and organ pipe cactus (*Stenocereus thurberi*) demonstrated that bats were important nocturnal pollinators of cacti (Alcorn et al., 1959; McGregor, Alcorn, and Olin, 1962). Recent studies have increased the list of chiropterophilous species of cactus from North, Central, and South America with details of the bat-plant interaction. Among these species are *Weberbauerocereus weberbaueri* (Sahley, 1995), *Stenocereus griseus*, *Subpilocereus repandus* (Petit, 1995a), *Stenocereus thurberi*, *Carnegiea gigantea*, *Pachycereus pringlei* (Fleming et al., 1994; Fleming, Tuttle, and Horner, in press), and *Neobuxbaumia tetetzo* (Valiente-Banuet et al., 1996).

Effectiveness of bat pollination and degree of plant specialization on these pollinators are still open ques-

tions. Relatively low values of fruit:flower ratio and high levels of ovule and seed abortion in chiropterophilous species (Sutherland, 1986; Ramírez, 1995) are partial evidence of the apparently low effectiveness of these pollinators in some species. The presence of mixed-species loads of pollen on bats (Baker, 1973; Heithaus, Opler, and Baker, 1974; Heithaus, Fleming, and Opler, 1975; Gould, 1978; Lemke, 1984), the disproportionate size between a bat and a stigma (Hokche and Ramírez, 1990), and the active consumption of pollen by several nectar-specialized species (Howell, 1979; Soriano, Sosa, and Rossel, 1991) are some of the arguments that could be used to support the low bat pollination effectiveness hypothesis. On the other hand, bats have been identified as very active and regular flower visitors of many plant species, transporting abundant pollen loads on different parts of their bodies (Heithaus, Opler, and Baker, 1974; Sazima and Sazima, 1977, 1978; Howell, 1979; Eguiarte, Martínez del Río, and Arita, 1987). Fleming, Tuttle, and Horner (in press) studied in detail the pollination effectiveness of bats in Mexican columnar cacti and found convincing evidence that one species of nectar-feeding bat, *Leptonycteris curasoae* (Phyllostomidae: Glossophaginae) is an effective pollinator of cardon (*Pachycereus pringlei*), saguaro (*Carnegiea gigantea*), and the organ pipe (*Stenocereus thurberi*). They found bats to be more effective pollinators per flower visit than birds and bees in saguaro and organ pipe, and almost equally effective as birds in cardon.

Genetic self-incompatibility and hermaphroditic sexual condition have been associated with relatively low levels of fruit set in many species of plants (Sutherland and

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Delph, 1984; Sutherland, 1986). In contrast, high levels of fruit and seed set have been reported for self-incompatible and hermaphroditic chiropterophilous columnar cacti, suggesting that in this group of plants bat pollination is highly effective (Alcorn et al., 1959; McGregor, Alcorn, and Olin, 1962; Fleming, Tuttle, and Horner, in press; Petit, 1995a; Sahley, 1995; Valiente-Banuet et al., 1996). The condition of solitary flowers, which occurs in all cacti, also contributes to an increase in the overall fruit set of these species (Ramírez and Berry, 1995).

In this paper we describe the pollination biology of five species of Venezuelan columnar cacti: *Stenocereus griseus*, *Pilosocereus moritzianus*, *Pilosocereus lanuginosus*, *Subpilocereus repandus*, and *Subpilocereus horispinus*. The two aims of this study were, first, to characterize and compare the pollination biology of these species, and second, to determine degree of effectiveness and relative importance of nectar-feeding bats as pollination agents of Venezuelan columnar cacti. Our results support the hypothesis that Venezuelan columnar cacti are specialized for bat pollination.

MATERIALS AND METHODS

Study area and species—The study sites were located in the arid zones of two coastal states of Venezuela: (1) "Pueblo de Mamo," 10 km west of "Simón Bolívar" International Airport (10° 53' N and 67° 02' W), Distrito Federal, on the central coast; and (2) "Península de Paraguaná" (11° 56' N–69° 56' W, and 11° 58' N–70° 01' W), northern portion of Falcón State, northwest coast of Venezuela. At Pueblo de Mamo field work was conducted between April and August 1990 and between January and April 1991; at Península de Paraguaná field work was conducted between September and December 1990. Pueblo de Mamo has a well-defined rainy season, with a mean annual precipitation of 512.7 mm, most rainfall occurring during July, November, and December (MARNR, 1991a). The average annual temperature is ~ 26.1°C (MARNR, 1991a). The topography of the area is characterized by low to moderate hills, 1000 m tall. At Península de Paraguaná rainfall occurs from October to mid-January, with a mean annual precipitation of ~ 450 mm (MARNR, 1991b). Mean annual temperature is ~ 28°C mm (MARNR, 1991b). Winds in the east and northeast direction are very frequent in most of the peninsula. Locations selected in Península de Paraguaná included extensive flatlands and a few small hills with low slopes. Both study sites are classified as tropical spiny scrub lifezone according to the Holdridge system of classification (Ewel, Madriz, and Tosi, 1976). In the "Map of Venezuelan Vegetation" (Huber and Alarcón, 1988), Pueblo de Mamo's vegetation is classified as "xerophilous littoral shrubs," and the sites studied at Península de Paraguaná correspond to the "xerophilous spiny shrubs" category.

The study included five species of columnar cacti: *Stenocereus griseus* (Tribe Pachycereeae) and *Pilosocereus moritzianus* (Tribe Pachycereeae) at Pueblo de Mamo, and *Subpilocereus repandus* (Tribe Cereaceae), *Subpilocereus horispinus* (Tribe Cereaceae), and *Pilosocereus lanuginosus* (Tribe Pachycereeae) in Península de Paraguaná. The latter species was only included in the comparative morphological analysis. With respect to flowering phenology at the study sites, *Stenocereus griseus* flowers throughout the year (A. Castillo, Centro de Botánica Tropical-UCV), *Pilosocereus moritzianus* between March and July (this study), *Subpilocereus repandus* between March and November, *Subpilocereus horispinus* between August and November, and *Pilosocereus lanuginosus* between July and October (R. Wingfield, BIOMA [Fundación Venezolana para la Conservación de la Naturaleza]; and this study). Other conspicuous elements of the vegetation in these areas include species of *Mellocactus*, *Mammillaria*, *Pereskia*, and *Opuntia* among the Cactaceae, *Acacia tortuosa* (Fabaceae), and *Agave cocuy* (Agavaceae).

This last species was only observed at Pueblo de Mamo, and its flowers are visited by nectar-feeding bats, hummingbirds, and bees.

Floral characteristics—We collected 28–31 mature flowers from a minimum of 15 different individuals of each species of cacti, and preserved them in 70% ethanol for morphological analysis. We described floral shape, odor, and perianth color from fresh material. The following flower measurements were recorded (Fig. 1): external and internal length, perianth diameter, distance from anthers (located at the top of floral tube) and stigma to base of floral tube, number of stamens/flower, number of ovules/flower, and number of seeds/open pollinated flower. The number of pollen grains/anther was estimated indirectly using Neubauer chambers with known dilution volumes of pollen grains obtained from three anthers of five flowers of each species of cactus (Lloyd, 1965). To estimate the number of pollen grains produced per flower, the number of pollen grains/anther was multiplied by the average number of anthers per flower. Pollen:ovule and seed:ovule ratios were estimated by dividing the mean number of pollen grains per flower and seeds produced per flower by the mean number of ovules per flower. The pollen grain area of contact ($A = \pi r^2$) was calculated measuring the diameter ($2r$) of a pollen grain with an optical microscope. The stigmatic area was estimated using image amplification and drawings of stigmas with a stereoscopic microscope and measuring the area with a LI-COR portable area meter (Model LI-3000, LI-COR, Lincoln, Nebraska). We estimated the maximum load capacity of pollen grains per stigma by dividing the stigmatic area by the pollen grain area of contact. That quantity reflects how many pollen grains could potentially make direct contact with the stigmatic surface; however, this method of calculation must be considered a first approach that might underestimate (overlapping of grains) or overestimate (empty spaces between adjacent grains) the maximum load capacity of pollen grains per stigma. We used 10–60 individuals of each species to determine temporal and spatial distribution of flowers per individual plant on a weekly basis. The monitoring included the number of unopened floral buds per plant per week, number of open flowers per plant per night, and the minimum and maximum flower heights (in metres) with respect to ground level.

Floral rewards—The process of anthesis was recorded from a total of 28–34 flowers from 20 to 30 different individuals of each species of cactus. Observations began in late afternoon (1700), when all the floral buds were completely closed. Nectar production (in millilitres) was determined for each species in 18–34 flowers from 18 to 25 different plants, by measuring nectar secretion from emasculated and bagged flowers with microcapillary tubes. Measurements were made each hour without replacement of the nectar extracted, starting before flower anthesis until the end of the secretion period. Flowers included in this analysis were temporally distributed over > 45 d for each species. We estimated the total nectar production per plant per night by multiplying the average value of nectar production per flower per night times the average number of open flowers per plant per night. Nectar sugar concentration (percentage sucrose equivalent units) was measured in these flowers each hour starting at the beginning of secretion, using a Bausch & Lomb hand refractometer.

Floral visitors—Diurnal and nocturnal floral visitors were observed, captured, or photographed, and identified. Flower visitation behavior of bats was studied and described in detail by standing ~ 2 m from the base of the cactus in flower. We recorded duration and visitation behavior, and calculated the percentage of bat visits to individual flowers in alternate intervals of 30 min from total number of visits per flower per night. Bat visitation was recorded from sunset until bats ceased foraging. Total number of bat visits per flower per night was calculated by adding the number of visits recorded in each interval of 30 minutes over the night and averaged over all flowers considered per species. The maximum number of bats visiting simultaneously a plant during the night was also determined by direct observation and averaged over all

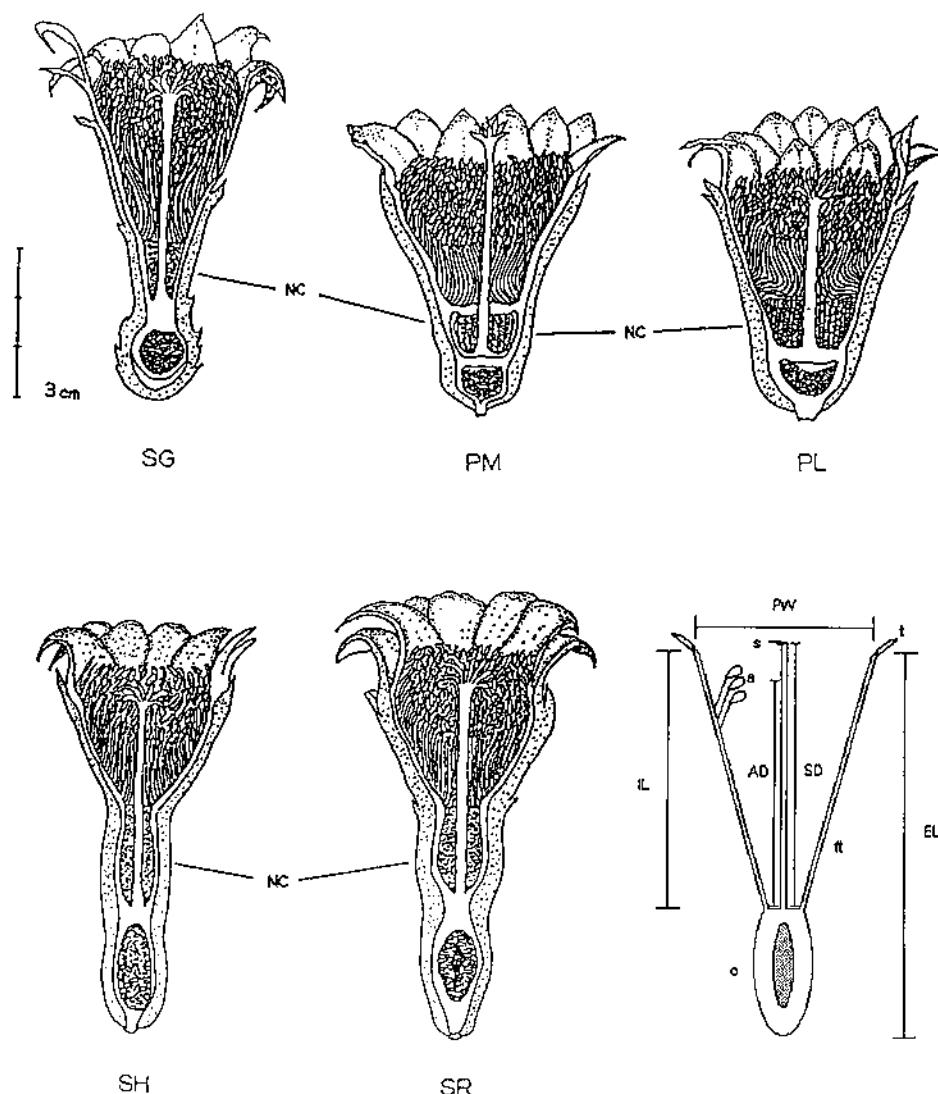


Fig. 1. Floral diagrams of five Venezuelan columnar cacti species and schematic representation of mature floral bud showing floral measurements studied. *Figure Abbreviations:* SG, *Stenocereus griseus*; PM, *Pilosocereus moritzianus*; PL, *Pilosocereus lanuginosus*; SH, *Subpilocereus horrispinus*; SR, *Subpilocereus repandus*; NC, nectar chamber; EL, external length; IL, internal length; PW, perianth width; SD, stigma height; AD, anthers height; a, anthers; s, stigma; t, tepal; ft, floral tube; and o, ovary.

plants considered per species. For duration, visitation behavior, and frequency of visitation we used a total of 13–24 flowers from at least ten different individuals of each species of cactus.

Breeding system and pollinator exclusion treatments.—Five different pollination treatments were applied to 17–58 flowers of each species to determine its sexual system: (1) natural pollination (flowers exposed to all pollination agents), (2) self-pollination without manipulation (bagged flowers isolated from all visitors), (3) induced self-pollination (flowers hand-pollinated with their own pollen and bagged), (4) cross-pollination (bagged flowers hand-pollinated with pollen from plants of the same species separated from the focal females by at least 30 m), and (5) agamospermy (bagged emasculated flowers). Hand-pollination was performed by rubbing vigorously a cluster of anthers of one flower against the stigma of the focal female. Self- and cross-pollination treatments were repeated on each flower at three different times during the night: 2000, 2200, and 0100 to guarantee stigma receptivity and pollen viability. These times correspond, respectively, to 1-, 3-, and 6-h old pollen grains (after flower opening). No more than three flowers of the

same individual were used for each test, except in *S. horrispinus*, a rare species present in relatively low density, in which up to six flowers from the same individual were used for each treatment.

We conducted exclusion experiments to determine the relative importance of bats as pollinators in each species of cactus. Thirty-one to 38 flowers from each species were isolated from visiting bats by surrounding them with spherical wire enclosures 20 cm in diameter. These enclosures had enough space between wires to permit visitation by moths, hawkmoths, hummingbirds, bees, and other potential pollinators, but precluded visitation by bats. Bees and hummingbirds were observed visiting flowers isolated from bats without problem. We determined the fruit:flower ratios for all treatments. The index of self-incompatibility (ISI) (fruit:flower ratio via selfing divided by fruit:flower ratio via out-crossing) was calculated (Bullock, 1985).

Statistical analyses.—Variables were compared among species using one-way ANOVAs and the Spjøtvoll and Stoline's test for unequal sample sizes for post hoc comparisons of means. If assumptions of the ANOVA were not met, then data were transformed to their natural

TABLE 1. Floral characteristics of the five species of columnar cacti. Data are means (± 1 SE). Species: *Stenocereus griseus* (SG), *Pilosocereus moritzianus* (PM), *Pilosocereus lanuginosus* (PL), *Subpilocereus repandus* (SR), and *Subpilocereus horrispinus* (SH). Test: one-way ANOVA (F), Kruskal-Wallis ANOVA (H). Roman numbers indicate results of post hoc comparisons.

Character	N	SG	PM	PL	SR	SH	Test
External length (cm)	22–26	5.1 ^{II} (0.15)	4.3 ^I (0.06)	4.2 ^I (0.15)	8.1 ^{IV} (0.14)	5.9 ^{III} (0.12)	$H = 93.3$ $P < 0.001$
Internal length (cm)	20–26	3.5 ^I (0.11)	3.5 ^I (0.09)	3.6 ^I (0.13)	5.4 ^{III} (0.16)	4.4 ^{II} (0.08)	$F = 52.2$ $P < 0.001$
Perianth width (cm)	22–26	2.1 ^I (0.04)	2.5 ^{II} (0.02)	2.3 ^I (0.06)	2.2 ^I (0.04)	2.1 ^I (0.04)	$H = 33.9$ $P < 0.001$
Anther height (cm)	17–25	3.6 ^I (0.15)	3.3 ^I (0.13)	3.1 ^I (0.11)	4.4 ^{II} (0.14)	4.6 ^{II} (0.11)	$F = 23.89$ $P < 0.001$
Stigma height (cm)	17–25	3.6 ^I (0.07)	4.7 ^{IV} (0.04)	4.0 ^{III} (0.16)	4.5 ^{IVIII} (0.12)	4.2 ^{III,III} (0.09)	$F = 40.8$ $P < 0.001$
Pollen grain area ($\times 10^{-5}$ cm ²)	30	3.7 ^{III} (0.05)	3.5 ^{II} (0.09)	2.8 ^I (0.05)	3.4 ^{II} (0.07)	3.3 ^{II} (0.05)	$F = 45.7$ $P < 0.0001$
Stigma area (cm ²)	18–23	2.4 ^{III} (0.16)	1.0 ^I (0.05)	1.1 ^I (0.04)	1.4 ^{II} (0.06)	2.3 ^{III} (0.10)	$F = 56.2$ $P < 0.0001$
Maximum number pollen grains/stigma ($\times 10^4$)	18–23	6.5 ^{III} (0.42)	2.9 ^I (0.14)	3.9 ^{II} (0.16)	4.1 ^{II} (0.21)	6.8 ^{III} (0.29)	$F = 164.7$ $P < 0.0001$
Number of stamens/flower	21–33	1180 ^{III} (55.0)	896 ^{II} (26.1)	797 ^{II} (28.2)	1295 ^{III} (35.6)	687 ^I (16.1)	$F = 55.3$ $P < 0.0001$
Number pollen grains/flower ($\times 10^5$)	21–33	17.2 ^{III} (0.81)	21.6 ^{IV} (0.63)	13.5 ^{II} (0.47)	16.6 ^{III} (0.46)	10.0 ^I (0.24)	$F = 78.8$ $P < 0.0001$
Number ovules/flower	28–31	1695 ^I (86.7)	3555 ^{II} (105.8)	4551 ^{III} (196.9)	1574 ^I (67.0)	1441 ^I (56.6)	$F = 153.4$ $P < 0.0001$
Number seeds/flower	15–27	1581 ^{II} (62.2)	2496 ^{III} (165.3)	—	1483 ^{II} (93.0)	1123 ^I (51.6)	$H = 35.9$ $P < 0.0001$
Pollen: ovule ratio	—	1016	607	296	1054	691	—
Seed: ovule ratio	—	0.93	0.70	—	0.94	0.78	—

logarithms. One-way Kruskal-Wallis ANOVA was used when the assumptions of the parametric ANOVA were not met even with log transformation of values. Nocturnal patterns of nectar production and nectar sugar concentration were compared between pairs of species using product-moment correlation analysis. Temporal patterns of bat visitation to flowers were compared between pairs of species using Kolmogorov-Smirnov two-sample tests. Product-moment correlation analyses were also conducted to examine associations between nectar secretion rates, sugar nectar concentration, and frequency of bat visitation.

RESULTS

Floral characteristics and reward availability—Qualitative and quantitative floral traits of the five species of columnar cacti studied were very similar (Fig. 1). Floral tubes were greenish externally except in *Stenocereus griseus*, in which the dominant color was purple-brown. The dominant color of the petaloid segments was white for all species but *S. griseus*, in which the perianth was pinkish and could be considered visually attractive to diurnal visitors. A characteristic odor similar to decomposed vegetables was detected in different intensities in each species but *S. griseus*, in which a more fragrant aroma could be distinguished. Flowers were funnel-shaped, with thick walls of fleshy to leathery tissue surrounding the sexual organs. All of these characteristics correspond to the classic syndrome of chiropterophily (van der Pijl, 1961; Faegri and van der Pijl, 1979).

Even though statistically significant interspecific differences were detected in the morphological characteristics of the flowers, these differences were small in absolute magnitude (Table 1); therefore we conclude that these species have a common floral morphological pattern. The distance between the stigma and the base of the

hypanthium was not significantly different from the distance between the top anthers and the base of the hypanthium in *S. griseus*, *S. repandus*, and *S. horrispinus* ($U = -0.020$, $P = 0.98$; $U = 0.404$, $P = 0.68$; $U = -1.82$, $P = 0.069$, respectively). On the other hand, in *Pilosocereus lanuginosus* and *P. moritzianus* the stigma was considerably exserted ($U = 6.05$, $P < 0.0001$; $U = 3.21$, $P < 0.0013$, respectively) and significantly higher than the anthers; therefore, the former three species are considered nonherkogamous and the latter two herkogamous.

Flowers of all species are hermaphroditic. As in the case of morphological measurements, significant interspecific statistical differences were detected in all reproductive variables (Table 1). The magnitudes of these differences were relatively small, indicating that a common suite of reproductive features characterizes this group of cacti. The pistil in all species has a single long central style with a multilobed stigma (10–14 lobes) surrounded by a ring of numerous stamens (>600 stamens/flower). Estimated pollen production per flower always exceeded one million grains. The estimated maximum (± 1 SE) load of pollen grains that the stigma could potentially hold was very high for all species ($2.9 \times 10^4 \pm 0.14 \times 10^4$ – $6.8 \times 10^4 \pm 0.29 \times 10^4$ pollen grains/stigma). The number of ovules produced per flower was relatively high for all species, with mean values always > 1000. The highest values occurred in *P. moritzianus* and *P. lanuginosus*. The pollen:ovule ratio was relatively variable among species, with extreme low and high values in *P. lanuginosus* (296) and *S. repandus* (1054), respectively. The average seed set per flower in all species but *P. lanuginosus* (data not available) was > 70% of the total number of ovules per flower.

TABLE 2. Floral availability in terms of spatial location on the plant, floral bud production, and number of open flowers per plant per night in five species of columnar cacti. Data are means (± 1 SE). Species: *Stenocereus griseus* (SG), *Pilosocereus moritzianus* (PM), *Pilosocereus lanuginosus* (PL), *Subpilocereus repandus* (SR), and *Subpilocereus horrispinus* (SH). Test: one-way ANOVA (F), Kruskal-Wallis ANOVA (H). Roman numbers indicate results of post hoc comparisons.

Availability	N	SG	PM	PL	SR	SH	Test
Flower height (m)	38–60	2.8 ^{II,III} (0.14)	2.6 ^{II} (0.16)	2.9 ^{II,III} (0.18)	3.3 ^{III} (0.18)	2.0 ^I (0.18)	$H = 32.6$ $P < 0.001$
No. flower buds-plant ⁻¹ ·week ⁻¹	31–59	8.6 ^I (1.11)	11.4 ^I (2.59)	9.7 ^I (1.72)	10.8 ^I (1.57)	8.6 ^I (1.05)	$F = 1.2$ NS ^a
No. flowers open-plant ⁻¹ ·night ⁻¹	42–162	1.4 ^I (0.05)	2.3 ^{II} (0.28)	4.4 ^{III} (0.60)	2.0 ^{II} (0.14)	2.4 ^{II} (0.24)	$H = 67.1$ $P < 0.001$

^a NS $P > 0.05$.

The five species were also similar in terms of spatial and temporal floral availability (Table 2). Flower distribution on the branches was apical or lateral, with average heights ranging from 1.96 to 3.33 m depending on the species. *S. horrispinus* was the only species with flowers at ground level due to the decumbent nature of its branches. *S. griseus* was the only species with flowers located primarily at the apex of the main branches. Plants of all species contained similar numbers of floral buds at the time of census. The average values were based on ~ 2 mo of weekly monitoring for each of the species. All species showed a relatively low number of flowers in anthesis per plant per night, with average numbers ranging from 1.4 to 4.4. With respect to temporal availability, anthesis was crepuscular and synchronous in all species. Peak anthesis in all species occurred between 1830 and 1930. Stigma receptivity and anther dehiscence occurred simultaneously with anthesis. Flowers remained open the entire night and the next morning except for *S. griseus*, in which flowers closed before sunrise. Although no systematic monitoring of pollen availability over time was conducted in this study, we observed that most of the pollen loads had been removed from the anthers by 0300 in the morning. Flowers were in advanced state of withering 24 h after anthesis.

Floral rewards—Nectar secretion started before anthesis in all species. The rate of nectar secretion increased abruptly after flowers opened and did not decrease until almost midnight (Fig. 2A). Maximum average rates of nectar secretion per flower occurred before midnight and were 0.126 mL/h at 2100 for *S. griseus*, 0.180 mL/h at 2300 for *P. moritzianus*, 0.164 mL/h at 2300 for *S. repandus*, and 0.123 mL/h at 2200 for *S. horrispinus*. After the peak, nectar secretion decreased gradually until 1–2 h before sunrise, when it reached zero. Patterns of nectar secretion over the night were very similar in all four species of cacti. Results of a correlation analysis between species indicate that, for all pairs compared, temporal patterns of nectar production were highly correlated ($r \geq 0.88$, $P \leq 0.001$). Total nectar production per flower per night exceeded 0.5 mL in each species (Table 3), with average values ranging from 0.671 ± 0.272 to 1.091 ± 0.452 mL · flower⁻¹ · night⁻¹. Estimated values of total nectar production per plant per night ranged from 1.0 mL to 2.5 mL for the different species.

The average values of nectar sugar concentration varied from 18.0 to 20.7% (sucrose equivalent units) for all species (Table 3), and the general pattern of variation in

nectar sugar concentration over the night was similar for all species (Fig. 2B). Results of a correlation analysis between species indicate that temporal patterns of nectar concentration were significant only between three pairs of species, *P. moritzianus*–*S. repandus* ($r = 0.72$, $P \leq 0.019$), *S. repandus*–*S. horrispinus* ($r = 0.86$, $P \leq 0.0016$), and *S. repandus*–*S. griseus* ($r = 0.71$, $P \leq 0.013$). In *S. griseus*, *S. repandus*, and *S. horrispinus*, nectar sugar concentration increased to a peak before decreasing; in contrast, sugar concentration did not increase in *P. moritzianus*, because the highest values for this species were recorded at the beginning of nectar secretion. In general terms, both nectar secretion and nectar sugar concentration patterns were similar in all species of cacti. Both variables were highly correlated in *S. griseus*, *S. repandus*, and *S. horrispinus*, but not in *P. moritzianus* (Table 4).

Floral visitors and visitation patterns—Bats were the most important floral visitors in all cacti. Two species of nectar-feeding bats associated with arid and semiarid environments were identified, the lesser long-nosed bat (*Leptonycteris curasoae* Miller) and the long-tongued bat (*Glossophaga longirostris* Miller), both in the subfamily Glossophaginae of the Phyllostomidae. Hawkmoths (Sphingidae) were rarely observed visiting cactus flowers, and then only those of *P. moritzianus* and *S. griseus* at Pueblo de Mamo. Visits of these insects lasted less than one second, with a frequency of visitation of 1 visit · flower⁻¹ · night⁻¹. At sunset (1900–1930), visits by *Megalopta* sp. (Hymenoptera: Halictidae) were observed at flowers of *P. moritzianus* and *S. horrispinus* at both study sites. Visitation by these bees was rarely observed and lasted from 5 to 20 min/flower. Visitation by hummingbirds occurred before sunset (1800–1900) and after sunrise (first hours in the morning). Two species visited *S. griseus* and *P. moritzianus* at Pueblo de Mamo, the Buffed Hummingbird (*Leucippus fallax*) and the White-Vented Plumbeater (*Chalibura buffonii*), while only the former visited cactus flowers at Península de Paraguán. Floral visits by hummingbirds lasted from 30 s/flower to 2 min/flower. These birds seemed to visit flowers more frequently than insects. They either landed on the perianth or hovered in front of the flowers. In both cases, birds introduced their beaks or only part of the head into the flowers. Although frequency of visitation to cactus flowers was not systematically studied for hummingbirds, these birds were less frequent visitors of columnar cacti than bats.

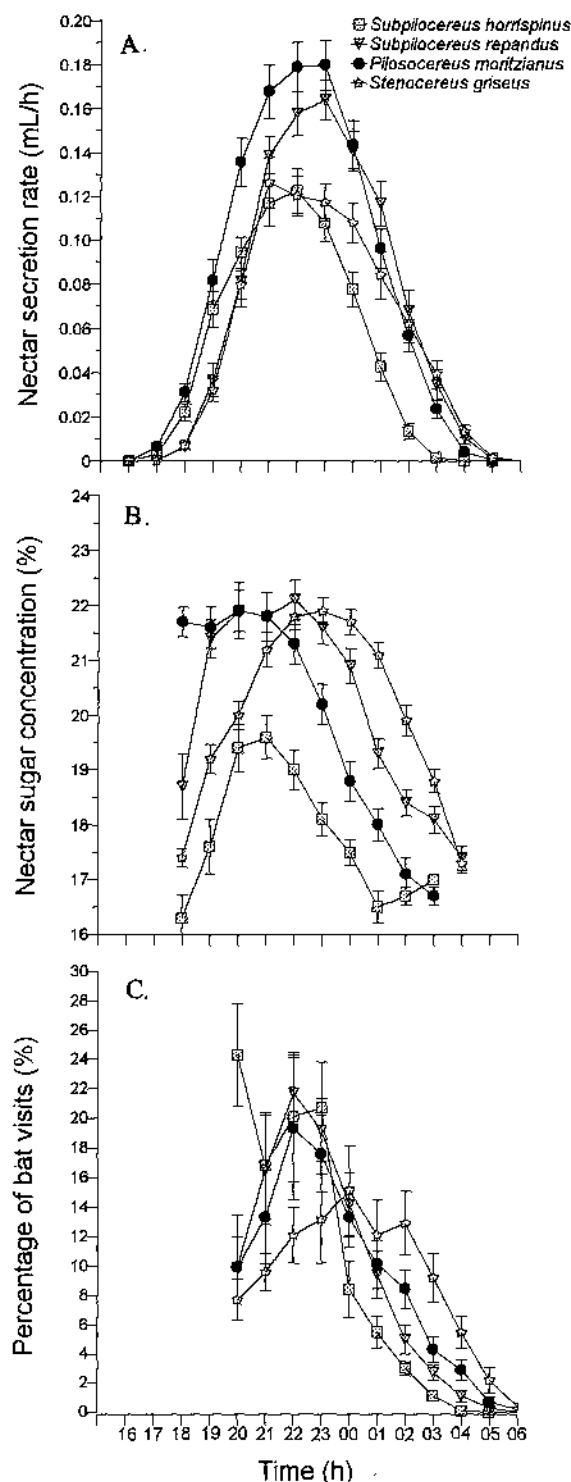


Fig. 2. Temporal patterns of nectar secretion in mL/h (A), nectar sugar concentration in percentage of sucrose equivalents (B), and bat visitation to flowers in percentage of visits from total number of visits per flower per night (C); in flowers of *Stenocereus griseus* (SG), *Pilosocereus moritzianus* (PM), *Subpilocereus repandus* (SR), and *Subpilocereus horrispinus* (SH). Data are means (± 1 SE). For nectar production $N = 18$ in SG, $N = 34$ in PM, $N = 30$ in SR, and $N = 28$ in SH; for nectar sugar concentration, $N = 17$ in SG, $N = 23$ in PM, $N = 27$ in SR, and SH; for percentage of visitation $N = 19$ in SG, $N = 18$ in PM, $N = 13$ in SR, and $N = 24$ in SH.

In all species, visits by bats started after sunset (1900–1930), and increased in frequency until almost midnight. The average number of floral visits ranged from 27 to 78 visits \cdot flower $^{-1}$ \cdot night $^{-1}$ (Table 3); floral visitation frequency was highly variable within all species. Peak rates of visitation occurred near midnight, after this peak, frequency of visits decreased to zero at 0500–0600 (Fig. 2C). The pattern of frequency of flower visitation over the night was very similar in the four species of cactus. Results of the Kolmogorov-Smirnov two sample-test indicate that, for all pairs of species compared, the estimated extreme differences were ≤ 0.40 ($P \geq 0.18$).

Bat visits were brief, most of them lasting < 2 s ($N = 24$). Two kinds of visitation behaviors were identified, hovering and grasping (hanging in front of the corolla and supporting bat's mass on its thumbs). Bats hovered in 83–100% of the visits to the different species of cacti and grasped flowers in a maximum of 17% of the visits ($N = 50$ visits) in the case of *P. moritzianus*. Bats introduced their heads into the floral tube, making contact with both stigma and anthers, and licking nectar from the nectar chamber. Visits were made by a single bat or by a group belonging to the same, or in some cases, different species. The number of bats in a group averaged 2 ± 1 ($N = 18$) at *P. moritzianus*, 3 ± 1 ($N = 19$) at *S. griseus*, 3 ± 1 ($N = 13$) at *S. repandus*, and 6 ± 3 ($N = 24$) at *S. horrispinus*. Even though several bats could be using the same flowers, no aggressive interactions between individuals were detected. The apparent temporal pattern of bat visitation to a flowering plant seemed to be cyclical. Although no formal data were taken to corroborate this observation, we noticed time periods with several visits alternated with time periods without visits.

In general, temporal patterns of nectar production and nectar sugar concentration and the relative frequency of flower visitation by bats were similar in all species of columnar cacti. Periods of high frequency of floral visitation corresponded to periods of high nectar production and sugar concentration. Similarly, decreasing frequencies of floral visits corresponded to decreasing values of sugar concentration and nectar production. Correlation analyses revealed that increases and decreases in the relative frequency of floral visitation by bats were significantly correlated with increases and decreases in rates of nectar production, but were comparatively less correlated with variation in nectar sugar concentration (Table 4). These results suggest that nectar volume has a greater effect on bat visitation frequencies than nectar quality.

Breeding systems and effective pollinators—Based on the Index of Self-Incompatibility (ISI) (Bullock, 1985), *S. griseus*, *S. repandus*, and *S. horrispinus* are self-incompatible (ISI = 0) (Table 5). In *P. moritzianus* only some fruits were produced from self-pollinated flowers (fruit:flower = 0.22; ISI = 0.35). According to the ISI value, this species should be considered partially self-compatible, however, fruits produced from selfing did not reach maturity. None of the species produced fruit in the self-pollination treatment without manipulation (bagged flowers). Fruit:flower ratios under natural pollination ranged from 46 to 76%, and seed:ovule ratios ranged between 70 and 94% (Table 1). Highest values of seed:ovule ratios were associated with highest values of pol-

TABLE 3. Total nectar secretion per flower per night, average nectar sugar concentration (sucrose equivalent units) over the night, and number of bat visits per flower per night. Data are means (± 1 SE). Species: *Stenocereus griseus* (SG), *Pilosocereus moritzianus* (PM), *Pilosocereus lanuginosus* (PL), *Subpilocereus repandus* (SR), and *Subpilocereus horrispinus* (SH). Test: one-way ANOVA (F), Kruskal-Wallis ANOVA (H). Roman numbers indicate results of post hoc comparisons.

Variable	N	SG	PM	SR	SH	Test
Nectar secretion · flower ⁻¹ · night ⁻¹ (mL)	18–34	0.792 ^{II} (0.053)	1.091 ^{II} (0.078)	0.958 ^{II} (0.068)	0.671 ^I (0.051)	$F = 6.90$ $P < 0.001$
Nectar sugar concentration (%)	17–27	20.7 ^{II} (0.3)	20.1 ^{II} (0.3)	20.4 ^{II} (0.3)	18.0 ^I (0.3)	$F = 17.4$ $P < 0.0001$
Number of bat visits · flower ⁻¹ · night ⁻¹	13–24	27 ^I (4.1)	41 ^{II} (7.1)	70 ^{III} (5.3)	78 ^{III} (10.8)	$H = 23.5$ $P < 0.0001$

len:ovule ratios, and lowest values of seed:ovule ratio were associated with lowest pollen:ovule values (Table 1). On the contrary, fruit:flower ratios under natural pollination did not show a consistent association with values of the pollen:ovule ratio (Tables 1, 5). Values of the fruit:flower ratio for the cross-pollination test exceeded 0.50 for all species (Table 5) and were not statistically different from values of the natural pollination treatment: *P. moritzianus* ($X^2 = 0.53$; $df = 1$; $P = 0.46$), *S. repandus* ($X^2 = 0.37$; $df = 1$; $P = 0.54$), *S. horrispinus* ($X^2 = 0.004$; $df = 1$; $P = 0.95$), and *S. griseus* (0.53) ($X^2 = 2.07$; $df = 1$; $P = 0.15$). These results indicate that fruit set in these species is not pollen limited. Even in *P. moritzianus*, which is partially self-compatible, the fruit:flower ratio via cross-pollination was almost twice as high as the fruit:flower ratio via self-pollination. In addition to this, the high values of seeds produced per flower under natural pollination seem to indicate high effectiveness in the deposition of pollen grains on the floral stigmas.

Results of the bat exclusion test (Table 5) showed that the proportion of flowers producing fruit decreased drastically (close to 0) in all species when bats were excluded. Differences in fruit:flower ratios under natural pollination and the bat exclusion treatments support the hypothesis that bats are acting as the main pollinator agents of these columnar cacti. Other agents, such as hummingbirds, moths, and bees appear to have a trivial effect as pollinators in this group of plants.

DISCUSSION

Our results support the hypothesis that the reproductive strategy of five species of Venezuelan columnar cacti involves a bat-specialized plant-pollinator system, in which flower visitation by nectar-feeding bats is essential for the sexual reproductive success of these cacti. Floral traits,

spatial and temporal availability of flowers, and patterns of nectar and pollen presentation in these cacti closely correspond to the well-known pollination syndrome of chiropterophily (Baker, 1961, 1970, 1973; van der Pijl, 1961; Faegri and van der Pijl, 1979). The basic floral traits shared by the Venezuelan bat cacti are: robust floral structures, funnel-form floral tubes, ripe vegetable-like odor, external colors that are not attractive to diurnal visitors, numerous stamens, large amounts of pollen and nectar, and nocturnal anthesis. Several of these traits have been already described for other species of chiropterophilous cacti studied in detail (Alcorn et al., 1959; Alcorn, McGregor, and Olin, 1962; McGregor, Alcorn, and Olin, 1962; Murawsky et al., 1993; Petit, 1995a; Sahley, 1995; Valiente-Banuet et al., 1996; Fleming, Tuttle, and Horner, in press). Many more species of columnar cacti not yet studied (Bravo-Hollis, 1978) also seem to match the description mentioned above, suggesting that chiropterophily is a widespread pollination syndrome in the Pachycereeae and Cereeae tribes of the Cactaceae.

The Venezuelan columnar cacti studied restrict their rewards (nectar and pollen) almost exclusively to nocturnal visitors. These species share the same general strategy of nectar and pollen presentation to their floral visitors. Both floral resources were almost exclusively directed to bats. In all cases the highest levels of nectar production occurred during the first few hours after anthesis, when nectar-feeding bats have the highest energy demand after a diurnal period without feeding. This condition differs from the nectar production patterns found in other species of columnar cacti at the northern and southern limits of their distribution in the New World. In northwestern Mexico, *Pachycereus pringlei*, *Stenocereus thurberi*, and *Carnegiea gigantea* have nectar secretion patterns that, even though starting at night, continue during the next morning following anthesis (Fleming, Tuttle, and Horner,

TABLE 4. Correlation coefficients (r) from correlation analysis of frequency of bat visits (%), nectar secretion rates (mL/h), and nectar sugar concentration (% sucrose equivalents) in four species of columnar cacti. Flowers measured corresponded to different plants in each species. Species: *Stenocereus griseus* (SG), *Pilosocereus moritzianus* (PM), *Pilosocereus lanuginosus* (PL), *Subpilocereus repandus* (SR), and *Subpilocereus horrispinus* (SH).

Species	Nectar production vs. nectar concentration			Frequency of visits vs. nectar production			Frequency of visits vs. nectar concentration		
	r	N	P	r	N	P	r	N	P
SG	0.96	10	<0.001	0.82	11	<0.01	0.62	8	NS ^a
PM	0.45	10	NS ^a	0.94	11	<0.001	0.67	8	NS ^a
SR	0.71	10	0.015	0.98	11	<0.001	0.87	8	<0.01
SH	0.86	10	<0.001	0.95	11	<0.001	0.85	8	<0.01

^a NS $P > 0.05$.

TABLE 5. Fruit:flower ratio from each pollination treatment and bat exclusion experiment. ISI = proportion of fruit set via self-pollination/proportion of fruit set via cross-pollination.

Species	Treatment	No. of flowers	Fruit:flower ratio	ISI
<i>S. griseus</i>	Agamospermy	23	0.00	0.00
	Natural pollination	49	0.76	
	Self-pollination	24	0.00	
	Hand cross-pollination	17	0.53	
	Total exclusion	35	0.00	
<i>P. moritzianus</i>	Bat exclusion	34	0.00	0.35
	Agamospermy	22	0.00	
	Natural pollination	57	0.46	
	Self-pollination	18	0.22	
	Hand cross-pollination	13	0.62	
<i>S. repandus</i>	Total exclusion	30	0.00	0.00
	Bat exclusion	38	0.03	
	Agamospermy	25	0.00	
	Natural pollination	51	0.49	
	Self-pollination	25	0.00	
<i>S. horrispinus</i>	Hand cross-pollination	18	0.61	0.00
	Total exclusion	42	0.00	
	Bat exclusion	35	0.06	
	Agamospermy	29	0.00	
	Natural pollination	58	0.50	
	Self-pollination	25	0.00	
	Hand cross-pollination	17	0.53	
	Total exclusion	28	0.00	
	Bat exclusion	31	0.00	

in press). In Perú, flowers of *Weberbauerocereus weberbaueri* start nectar secretion in the afternoon (Sahley, 1995). Only species of columnar cacti distributed within tropical limits seem to restrict floral rewards to nocturnal visitors. This is the case in *Neobuxbaumia tetetzo* in the Tehuacán Valley, México (Valiente-Banuet et al., 1996) and *Stenocereus griseus* and *Subpilocereus repandus* on Curacao (Petit, 1995b). Nectar volumes produced by flowers of the Venezuelan species were relatively high compared to other chiropterophilous plants (Voss et al., 1979; Lemke, 1984; Hokche and Ramírez, 1990). These volumes were exceeded only by species with dense inflorescences such as *Parkia* (Baker and Harris, 1957; Hopkins, 1984; Grunmeier, 1990) and by columnar cacti from northwestern Mexico, which produced an average of 1.1–2.0 mL per flower per night (Fleming, Tuttle, and Horner, in press). Nectar sugar concentration levels of the Venezuelan species fit the range commonly reported for other chiropterophilous species (Heinrich, 1975; Baker, 1978; Howell, 1979; Helversen and Reyer, 1984). Compared to the sugar concentration levels reported for the Mexican cacti (24–28%) (Valiente-Banuet et al., 1996; Fleming, Tuttle, and Horner, in press), the Venezuelan species had a relatively more dilute nectar. One possible explanation for this difference has to do with the pollinator agents of the different species and their nectar requirements. While Venezuelan cacti flowers produce nectar only at night, nectar in several Mexican species is also available to diurnal pollinators, including birds and bees (Fleming, Tuttle, and Horner, in press). In these species nectar sugar concentration might be a trade-off between demands of nocturnal and diurnal consumers. Bees have been frequently associated with flowers characterized by highly concentrated nectar (Gottsberger, Schrauven, and Linskens, 1984), while bats and hummingbirds have al-

ways been associated with relatively dilute nectar (Heinrich, 1975; Sazima and Sazima, 1977, 1978; Baker, 1978). In summary, even though nectar-feeding bats are the nocturnal pollinators of several species of columnar cacti, differences in timing of nectar secretion, volumes produced, and sugar concentration, suggest that these species differ in their degree of specialization for bat visitation. In this sense, Venezuelan columnar cacti can be considered among the more bat-specialized species.

Bats are the most common floral visitors of the Venezuelan columnar cacti studied. The temporal concordance between peaks of floral visitation, nectar production, and sugar concentration for all species suggests that reward presentation is the main factor influencing the pattern of visitation displayed by bats at these plants. This influence should be affected by the amount of reward offered per unit of time (rate of nectar production) and the quality of the reward (solute concentration). Results of the correlation analysis indicated a stronger association between bat visits and rates of nectar production than between bat visits and nectar sugar concentration. The average amount of nectar that can be obtained from a single flower per night (0.6–1.1 mL) is very low compared to the theoretical amount needed to meet the daily energy budget of *Leptonycteris curasoae yerbabuenae* in northern México (7.7–9.8 mL, ~40.2 kJ) (M. A. Horner, Texas Parks and Wildlife Department, personal communication). An average of two flowers were open per plant per night in the species studied, producing a maximum volume of ≤ 5 mL of nectar \cdot plant⁻¹ \cdot night⁻¹. The high demand for energy in nectar-feeding bats should promote visitation to many blooming individuals per night and probably a pattern of revisitation to previously used flowers.

During their visits to cactus flowers, bats function as effective pollinators. The main body parts involved in the pollination process are the head, neck, and shoulders, where most of the pollen is deposited. Production of large amounts of pollen by flowers of columnar cacti results in large amounts of pollen being deposited on the bats, therefore increasing the probability of deposition of numerous pollen grains on the floral stigmas. On the other hand, the relatively large stigmatic capacity of cactus flowers (up to five orders of magnitude of pollen grains can be held potentially on one stigma) guarantees the reception of enough pollen grains to fertilize most ovules. The deposition of large amounts of pollen on the stigmatic surface may promote male gametophytic competition (Stephenson and Bertin, 1983; Snow, 1986) between pollen grains from the same individual or different individuals and may possibly select for male gametophytes with higher rates of pollen tube growth (Cruden, 1977; Mulcahy, 1979; Feinsinger, 1987; Schlichting et al., 1987; Stephenson et al., 1988). If the amount of pollen deposited by bats on floral stigmas were high enough to promote sexual selection, then the service of this pollen vector could be interpreted as promoting fitter offspring.

Nectar that is continuously produced all night long encourages energy-demanding bats to visit many flowers during a long period of time, and to move between different flowers in order to satisfy their energy needs. This pattern of pollen movement, in addition to the high flight capacity of nectar-feeding bats (Sahley, Horner, and Fleming, 1993; M. A. Horner, Texas Parks and Wildlife Department, per-

sonal communication), guarantees that pollen will be transferred between genetically different plants. Under these circumstances, nectar-feeding bats are acting as appropriate pollinators of self-incompatible plants.

Obligate cross-fertilization was demonstrated for three of the species of cacti studied; only *P. moritzianus* was partially self-compatible. An emphasis on outcrossing is also suggested by observed values of the pollen:ovule ratio (296–1054). According to Cruden (1977) and Cruden and Miller-Ward (1981), these species should be considered between the “xenogamous facultative” and “xenogamous obligate” categories. The lowest values of pollen:ovule ratio were found in *P. moritzianus*, as expected because of its partial self-compatibility. Self-compatibility has been previously documented for two species of chiropterophilous columnar cactus, hermaphrodite individuals of *Pachycereus pringlei* with a selfing rate as high as 65% (Murawski et al., 1993), and *Weberbauerocereus weberbaueri*, with a selfing rate of 26% (mature fruit set) (Sahley, 1995); however, for *P. moritzianus* the herkogamous condition could be considered a physical mechanism promoting xenogamy. Another interesting observation from our results is that the seed:ovule ratios show certain correspondence with the pollen:ovule ratios. The highest values of seed:ovule ratio occurred in species with the highest pollen:ovule ratios. This result suggests that in multiovule species, independently of the mating system, high pollen:ovule ratios seem to increase the proportion of ovules successfully fertilized through an increase in the pollen loads produced; however, that relationship did not hold for the fruit:flower ratio.

According to the results of the bat exclusion experiments, fruit and seed production via natural pollination can be attributed almost exclusively to visitation by nectar-feeding bats in these species. Besides the exclusion experiments, field observations indicated that diurnal visitors are ineffective pollinators for one of three reasons: vector size and visitation behavior precludes pollination, visits rarely happened, or because time of visitation occurred before or after floral resource presentation. These results were consistent with low fruit set under bat exclusion found by Petit (1995a) in *Stenocereus griseus* (0%) and *Subpilocereus repandus* (10%) in Curaçao, and by Valiente-Banuet et al. (1996) in *Neobuxbaumia tetetzo* (0%) in Mexico. This obligate dependence on bats for sexual reproduction supports the thesis of an obligate mutualistic interaction between nectar-feeding bats and Venezuelan columnar cacti. One piece of evidence supporting this idea is the extensive geographic overlap between the Venezuelan columnar cacti and the distribution of *Lepidonycteris curasoae* and *Glossophaga longirostris* (Linares, 1986; Ponce, 1989). Geographic overlap between the components of a mutualistic interaction is evidence of a specialized interaction (Thompson, 1995). This character of obligate bat dependence contrasts with observations of Fleming, Tuttle, and Horner (in press) and Sahley (1995). Fleming, Tuttle, and Horner reported effective pollination by diurnal visitors in three Mexican columnar cacti, *Pachycereus pringlei*, *Stenocereus thurberi*, and *Carnegiea gigantea* with proportions of fruit set for diurnal pollination ranging from 18 to 68% in *Carnegiea gigantea*. Sahley also reported effective diurnal pollination in the Peruvian cactus *Weberbauerocereus weber-*

baueri, with percentages of mature fruit set for day pollination being >35%. Thus, strong dependency on bats as pollinators is not universal in columnar cacti.

A critical question concerning the bat-cactus interaction is how effective are nectar-feeding bats as pollinators of the Venezuelan columnar cacti? Several lines of evidence suggest that bats are effective pollinators. First, in terms of food diversity, there are few alternative resources besides columnar cacti that nectar-feeding bats could use in arid environments (Soriano, Sosa, and Rosset, 1991). This limited diversity of resources could force nectarivorous bats to rely heavily on few species of plants that offer predictable rewards in extreme environments. Second, the seed:ovule ratios under natural pollination were relatively high for all the species studied (0.70–0.98) compared to values found in species (no cacti) with other pollination modes (Ramírez, 1995). This result indicates that bats are depositing enough pollen on floral stigmas to fertilize most of the ovules. According to Ornduff (1970), stigmatic deposition of enough pollen grains to produce a complete set of seeds can be interpreted as a measure of effectiveness of the pollination system. Finally, percentages of fruit set commonly reported for self-incompatible chiropterophilous species are considerably lower (21–35%, Sutherland, 1986; N. Ramírez, Centro de Botánica Tropical-UCV) than values found in this study and in other studies of chiropterophilous columnar cacti (Petit, 1995a; Sahley, 1995). We suggest, however, that high bat pollination effectiveness should not be considered the only cause of the relatively high values of fruit set found in columnar cacti. Ramírez and Berry (1995) relate high levels of fruit and seed set with the condition of solitary flowers, which is the case in all species of columnar cacti. The allocation of plant resources should be relatively greater in solitary flowers compared to floral units in multiple-flowered inflorescences.

Based on levels of pollination effectiveness in the Venezuelan columnar cacti, we have demonstrated in this study that bats are the only reliable resource that these plants have for their sexual reproduction. Both Fleming, Tuttle, and Horner (in press) and Sahley (1995) have demonstrated decreased nocturnal fruit set in columnar cacti species due to limited populations of bat species in Mexico and Peru, respectively. During periods of bat scarcity, those cacti rely on effective alternate pollinators to promote outcrossing and to maintain genetic variation in their populations, but what would be the consequences if populations of nectar-feeding bats decreased in Venezuela? Which pollinators would maintain sexual reproduction and genetic variability in Venezuelan cacti? Overall, our results indicate that the mutualistic interaction between nectar-feeding bats and columnar cacti in Venezuela seems to be very specialized and consequences of a serious disturbance on either component could be definitive.

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