Pollination biology of two winter-blooming giant columnar cacti in the Tehuacán Valley, central Mexico

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In the neotropics, central Mexico and Venezuela, columnar cacti (mostly belonging to tribe Pachycereae) are pollinated mainly by bats. In the Tehuacán Valley 36 species of columnar cacti have their blooming peak almost simultaneously between April and June, and species with chiropterophilous pollination have been shown to be self-incompatible, fruiting only after bat pollination. Nectarivorous bats are abundant also during spring and summer, and migrate during autumn and winter. Two columnar cacti, *Pachycereus weberi* (tribe Pachycereae) and *Pilosocereus chrysanthus* (tribe Cereae), flower during winter and early spring facing an apparent scarcity of bats. We hypothesized that under this condition, these plants may resemble the columnar cacti in extratropical deserts where both bats and diurnal vectors can effect seed production. However, we found that these two plant species have white, long tubular flowers, are nocturnal, self-incompatible and produce fruits only after the visitation of four nectar-feeding bats and two frugivorous bats. We found that nectar-feeding bats have a small resident population in the Valley. In addition these cacti species grow along possible routes of bat altitudinal migration. A long, and possibly variable flowering season may be also related to low pollen vector density.

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Introduction

Giant columnar cacti have their centre of diversification in south-central Mexico, the Tehuacán Valley and the Balsas River Basin being the richest zones with 45 out of 70 species found in the whole country (Valiente-Banuet *et al.*, 1996). In these areas,

columnar cacti are dominant elements of the xerofile scrublands occurring in densities of about 1200 to 1800 individuals per ha (Valiente-Banuet *et al.*, 1996). Pollination and seed production in cacti are critical demographic processes since almost all the studied species are self-incompatible and therefore need animal vectors for fertilization (Alcorn *et al.*, 1961, 1962; Grant & Grant, 1979; Valiente-Banuet *et al.*, 1996). What is remarkable is that 60% of the 70 species of columnar cacti occurring in Mexico have a chiropterophilous pollination syndrome, and because of their ecological dominance, constitute an important resource for nectar-feeding bats (Valiente-Banuet *et al.*, 1996). Like giant columnar cacti, nectarivorous bats reach their centre of diversification in south-central Mexico (Valiente-Banuet *et al.*, 1996).

In extratropical deserts such as the Sonoran Desert, columnar cacti are pollinated by a variety of animals, including bats, birds and insects, and although their flowers show a chiropterophilous pollination syndrome (as defined by Faegri & van der Pijl, 1979), diurnal pollinators sometimes are the most effective (Alcorn *et al.*, 1961, 1962). In contrast, columnar cacti in intertropical deserts such as the Tehuacán Valley in Mexico (Valiente-Banuet *et al.*, 1996) and in Venezuelan deserts (Soriano *et al.*, 1991; Sosa & Soriano, 1992) are mostly pollinated by nocturnal visitors, such as nectar-feeding bats. It has been hypothesised that unpredictable pollinator activity is the main selective factor in maintaining an unspecialized floral biology, because bat populations may fluctuate in extratropical zones owing to the risks associated with latitudinal migration (Valiente-Banuet *et al.*, 1996). In the Tehuacán Valley and the Balsas River Basin, columnar cacti present a clear blooming peak with 36 species blooming between April and June (Rojas, 1996; Valiente-Banuet *et al.*, 1996) when nectar-feeding bats are more abundant and more diverse; three to five species and around 30 individuals can be caught in one night (Rojas-Martínez & Valiente-Banuet, 1996). However, some plant species flower during winter when bats are scarce, and only one to two species and around three individuals can be caught with the same netting effort (Rojas, 1996). We hypothesized that columnar cacti flowering during winter might have a more generalized pollination syndrome resembling those of extratropical deserts. This study reports a test of this hypothesis by analysing the pollination ecology and mating system of two columnar cacti which bloom during winter, *Pachycereus weberi* (Coult.) Backeb. and *Pilosocereus chrysacanthus* (F.A.C. Weber) Byles & Rowley syn. *Cephalocereus chrysacanthus* (F.A.C. Weber) Britton & Rose.

Materials and methods

Study sites

The *Pachycereus weberi* zone is located in the southern part of the Tehuacán Valley along alluvial fans in the vicinities of the towns of Coxcatlán, Calipan and Cuicatlán (18° 16' N, 97° 07' W) at 1000 m a.s.l. (Fig. 1). Mean annual precipitation is 440 mm and annual mean temperature is around 23·8°C (García, 1973). This area is covered by a dry woodland dominated by the columnar cacti *Pachycereus weberi* (Coult.) Buxb., *Neobuxbaumia tetetzo* (F.A.C. Weber) Backeb., *Stenocereus stellatus* (Pfeiff.) Riccob., *S. pruinosus* (Otto) F.Buxb. and *Escontria chiotilla* (F.A.C. Weber) Rose, and the trees *Prosopis laevigata* (Humb. & Bonpl. ex Willd.) M.C. Johnst., *Celtis pallida* Torr., *Bursera morelensis* Ramirez and *Ziziphus amolle* (Sessé & Moc.) M.C. Johnst.

Pilosocereus chrysacanthus is found in San Antonio Texcala, and in isolated patches in the semi-arid Valley of Zapotitlán (18° 20' N, 97° 28' W), at 1700 m a.s.l., a local basin of the Tehuacán Valley in the state of Puebla, Mexico (Fig. 1). It has an average rainfall of 380 mm, an annual mean temperature of 21°C, with rare frosts (García, 1973). Soils are rocky and derived from sedimentary and metamorphic rocks. The main vegetation type is arid tropical scrub (Rzedowski, 1978) in which the giant
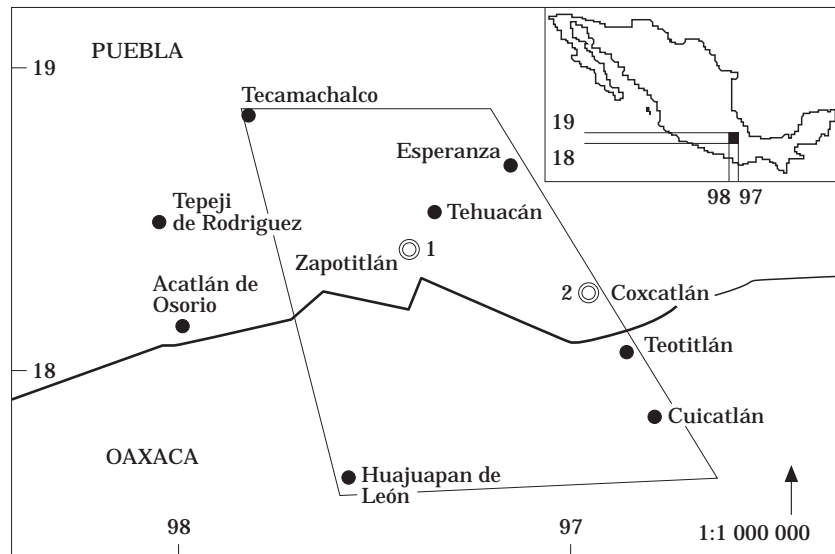
Figure 1. Study site locations of *Pilosocerus chrysacanthus* (1) and *Pachycereus weberi* (2).

columnar cacti *Pachycereus fulviceps* (F.A.C. Weber) D.F. Hunt syn. *Mitrocereus fulviceps* (F.A.C. Weber) Backeb. and *Pilosocereus chrysacanthus*, and the tree *Acacia subangulata* Rose constitute the most important physiognomic elements of the vegetation.

Abundance and flowering intensity

To determine the density of *Pachycereus weberi* and *Pilosocereus chrysacanthus* we recorded height and number of flowers and fruits for every individual along a 100 m by 10 m transect located at random in each study zone during January and March 1995. We defined flowering intensity at the frequency of potentially reproductive individuals, ≥ 2 m with flowers (Valiente-Banuet & Ezcurra, 1991). The number of flowers per adult per night for a total of 10 randomly selected individuals per species was counted during three different nights in order to determine the flower resource for nocturnal pollinators.

Floral biology

To describe floral biology, 10 flowers were selected at random from a total of 30 individual plants per species and total length, i.e. length from petal tip to flower base, external diameter at corolla apex, and internal diameter of floral tube at point of anther dehiscence measured (Fig. 2). In order to follow flower receptivity, we marked 10 buds in 10 individual plants. Every 2 h from flower opening to flower closing anther dehiscence and stigma turgidity was monitored.

The volume of nectar produced by *Pachycereus weberi* was measured in a further 10 flowers randomly chosen from among 30 individuals. Flowers were bagged before anthesis with mosquito netting and nectar accumulated during the night and day was measured with microcapillary tubes. Nectar production by *Pilosocereus chrysacanthus* was measured every 2 h, from 2200 to 1000h, using three flowers per selected hour

with microcapillary tubes. Sugar concentration was measured (nectar sample obtained at 0600h) with a hand-held refractometer (American Optical No. 9103).

Breeding system

To determine the breeding system and differential effectiveness of visitors in each species, 60 flower buds from a total of 30 plants were marked and bagged with mosquito netting during 1995. Ten flowers were assigned to each of the following treatments: (**1**) non-manipulated self-pollination: flower buds were bagged and monitored until they aborted or set fruit; (**2**) nocturnal pollination: flower buds were bagged before opening and after the flowers had opened they were exposed to nocturnal floral visitors by removal of the bag from 2000 to 0500h (1 h before sunrise). At 0500h the flowers were rebagged and monitored until abortion or fruit production; (**3**) diurnal pollination: flower buds were bagged and flowers exposed to diurnal visitors by removing the bag at 0600h until the flowers closed at ≈ 1000 h, when the flowers were rebagged and monitored until abortion or fruit production; (**4**) cross-pollination: flower buds were bagged and when opened the flowers were hand-pollinated using fresh pollen obtained from another plant; (**5**) self-pollination: flower buds were bagged and after the flowers had opened they were hand-pollinated using pollen obtained from the same flower; (**6**) unmanipulated open pollinated flowers: flowers were marked only and left until abortion or fruit production.
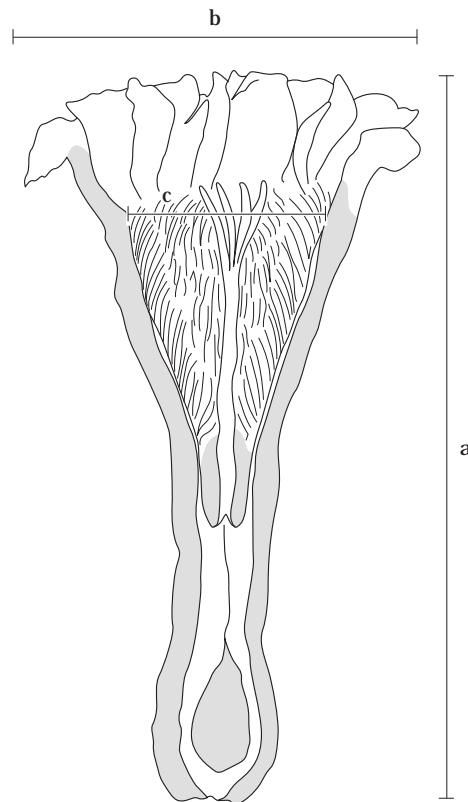

Figure 2. Sketch of the flower morphological measurements: (a) = total length, (b) = external diameter and (c) = internal diameter.

Bagged flowers were periodically monitored until abortion or fruit and seed maturation occurred, and the number of mature seeds per fruit was recorded.

Flower visitors

To identify nocturnal and diurnal visitors, four mist nets (12 m long × 3 m tall; separated by ≈ 100 m) were placed in a transect located at random in a high density area of *Pachycereus weberi*. Netting was carried out on nine moonless nights distributed throughout the blooming period during 1995 as follows: four nights in February, two in March, one in November and two in December. One additional netting was carried out during January 1996 (480 netting h). For *Pilosocereus chrysacanthus*, netting was done on two moonless nights during 1995: one night in March, one during April; and five moonless nights during 1996, two in April, two in May and one in June (336 netting h). Nets were opened at sunset (≈ 1900h) and closed in the morning (≈ 1000h). Nets were examined every 10 min at night and every 30 min during the day. In addition, we concurrently maintained a black light insect trap during the netting nights.

For each animal caught, pollen preparations were made by rubbing a cube of fuchsin-stained jelly (Beattie, 1971) over the bat's body. The cube was placed on a microslide, melted, and covered with a coverslip for later examination under the microscope. Pollen presence was regarded as proof of flower visitation. In addition, frequency of a given pollen species among visitors was considered as an indicator of the extent to which the plant was used. We later compared pollen grains from animal samples with those obtained directly from plants flowering in the area (each plant sample consisted of a mixture of pollen obtained from 10 individual plants). Bat faeces were also collected in order to obtain seeds and pollen.

Results

Pachycereus weberi is a profusely branched columnar cactus whose adults reach 10 m in height and 6 to 8 m in diameter. It is the dominant species in the study area with 150 adult (> 2 m tall) individuals per ha. Plants flowered from late November through February, with a few flowers present during March. Fruiting occurred from February to late March.

Pilosocereus chrysacanthus is a branched columnar cactus of approximately 4 m height with densities of 90 reproductive individuals per ha, occurring on top of limestone hills and igneous rock slopes. Plants flowered from January through April during 1995, but in 1996 flowering started during March. Fruits were present from mid March until May, although isolated individuals produced a few flowers and fruits from May to August.

Floral biology

Pachycereus weberi bore flowers 10·2 cm (S.D. = 0·54; $N = 10$) long, 4·9 cm (S.D. = 1·12; $N = 0$) external diameter and 3·0 cm (S.D. = 0·3, $N = 10$) internal diameter. Flowers were nocturnal, opening at dusk (*c.* 1900h) and closing in the early afternoon (*c.* 1400h) during winter, whereas during spring flowers close earlier (*c.* 0900h). Anthers and stigma were turgid throughout the night, but at dawn the stigma lost its turgidity in eight of the 10 observed flowers. The anthers and stigma of the remaining two flowers maintained their turgidity.

Nectar volume accumulated through the night (from opening until 0530h) was 3 ml (S.D. = 0·79; N = 10).

Pilosocereus chrysacanthus bore flowers 7·4 cm (S.D. = 0·44; N = 10) long, 5·8 cm (S.D. = 0·7; N = 10) external diameter and 4·1 cm (S.D. = 0·7; N = 10) internal diameter. Flowers were mainly nocturnal, opening at dusk (*c.* 1900h) and closing in the early morning (1000h). Anthers and stigma were turgid throughout the night, but at dawn the stigma lost its turgidity. Stigmas were turgid (1800h) before the flowers opened and protruded from the floral buds.

Nectar production was continuous during flower anthesis until they closed, and no evidence was found that nectar was reabsorbed if not consumed by visitors (Fig. 3). Sugar concentration was 21·2%.

Breeding system

Flowers of *Pachycereus weberi* that were either not manipulated and allowed to self, or were hand self-pollinated, did not produce seeds. Flowers visited by nocturnal pollinators produced an average of 1322·6 seeds per fruit (S.D. = 128·7; N = 10). Six of the 10 hand cross-pollinated flowers produced no seeds and the others produced an average of 760 seeds per fruit (S.D. = 521·5; N = 4). In contrast, flowers exposed only to diurnal pollinators produced no seeds. All of the 20 flowers (treatments 2 and 6) counted on the 10 plants produced fruits. This means that pollinators were 100% efficient and all flowers were pollinated.

Blooming was massive, with 100% of all the potentially reproductive individuals flowering at the blooming peak that occurred in February 1995, while only 10% of potentially reproductive individuals produced flowers during 1996.

Flowers of *Pilosocereus chrysacanthus* that were not manipulated but allowed to self or were hand self-pollinated did not produce seeds. Flowers visited by nocturnal pollinators produced an average of 1230·4 seeds per fruit (S.D. = 393·4; N = 10). Hand cross-pollinated flowers produced an average of 1014·5 seeds per fruit (S.D. = 148·4; N = 10). In contrast, flowers exposed only to diurnal pollinators produced no seeds.
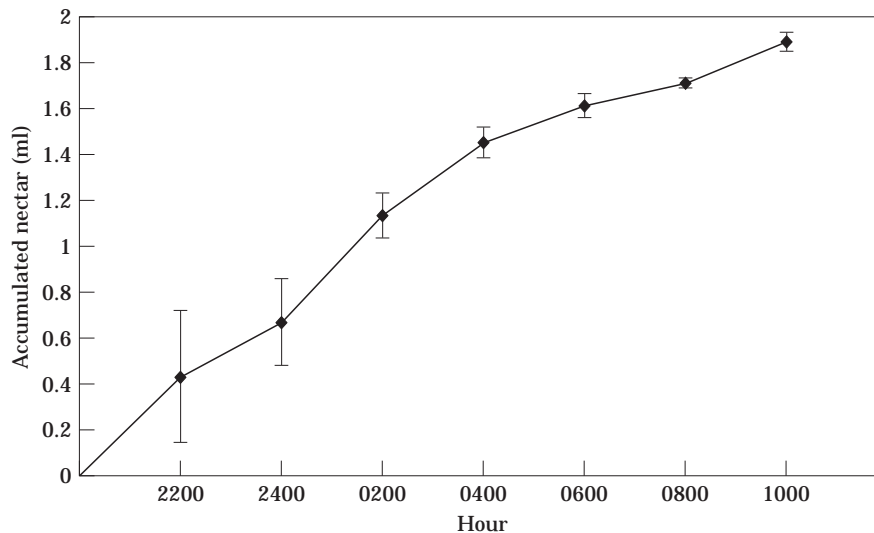

Figure 3. Accumulated nectar production of *Pilosocereus chrysacanthus* in the Tehuacán Valley. Bars indicate one standard deviation with respect to mean (N = 3 per hour registered).

All of the 30 flowers selected from 30 individual plants produced fruits, that is, pollinators were 100% efficient and all flowers were pollinated during 1995.

Blooming was massive, with 100% of all the potentially reproductive individuals flowering in the peak of blooming which occurred in late March 1995 and 1996.

Visitors

Eight bat species were caught during the flowering season of *P. weberi*: *Leptonycteris curasoae yerbabuenae* Martínez & Villa (*N* = 10), *Leptonycteris nivalis* Saussure (*N* = 6), *Choeronycteris mexicana* Tschudi (*N* = 3), *Artibeus jamaicensis yucatanicus* J.A. Allen (*N* = 23), *Sturnira lilium parvidens* Goldman (*N* = 6), *Glossophaga soricina handleyi* Webster & Jones (*N* = 1), *Artibeus intermedius* H. Allen (*N* = 1), and *Chiroderma salvini scopaeum* Handley (*N* = 1) (Table 1). All captures occurred between 1900 and 0550h.

The first six bat species bore pollen of *Pachycereus weberi*, and only *Leptonycteris curasoae* was recorded eating pollen, nectar and fruits of this columnar cactus simultaneously. Pollen was the dominant element in the faeces of *L. nivalis, L. curasoae, C. mexicana* and *G. soricina*, while the faeces obtained from the other bat species were mainly vegetal. Pollen loads obtained from the bodies of *Artibeus jamaicensis* and *Sturnira lilium* consisted of very few pollen grains per individual and with very few individuals carrying pollen (Table 1), contrasting with a high frequency and heavy pollen loads obtained from *L. nivalis, L. curasoae, C. mexicana* and *G. soricina*.

Diurnal visitors included hummingbirds (five *Cynanthus latirostris* Gould) and bees (*Apis melifera* L. and *Trigona* sp). Four hummingbirds and all the bees captured were carrying pollen of *P. weberi*.

Four bat species were caught during the flowering season of *Pilosocereus chrysacanthus*. *Leptonycteris curasoae, L. nivalis* and *Choeronycteris mexicana* bore pollen of *Pilosocereus chrysacanthus* and no seeds of this plants were found in the faeces. Another frugivorous bat species, *Sturnira lilium* Goldman, was caught and was also bearing pollen. The number of individual bats caught are shown in Table 1.

Diurnal visitors included four hummingbirds (*Cynanthus latirostris*) and honeybees (*Apis melifera*), all of them carrying pollen grains of *P. chrysacanthus*.

Discussion

The two plant species are successfully pollinated entirely during night-time. Bats were the only animals capable of pollinating these columnar cacti, since no other visitors were detected at night. Diurnal visitors such as hummingbirds and bees acted only as nectar robbers as they consumed the nectar remaining from the nocturnal secretion but did not pollinate the flowers. This may be due to floral morphology. The small visitor hummingbirds (exposed culmen of *Cynanthus latirostris* mean = 21·19 ± 1·41 mm, *N* = 34, taken from Arizmendi, 1987) must insert part of their bodies in the flowers in order to reach nectaries. In doing so, birds may not contact the stigma as the partially opened flower tube is almost 3 cm wide in *Pachycereus weberi* and almost 4 cm in *Pilosocereus chrysacanthus*. However, it seems that specialization for bat pollination in these cacti is related to function as well as morphology because stigmas are not receptive during the day. Thus specialization for bat pollination resembles that found in other columnar cacti from central Mexico in which the blooming period occurs when bats are very abundant in the Valley (Valiente-Banuet *et al.*, 1996; Valiente-Banuet *et al.*, in press); there are similar findings for other plants in which a wide array

Table 1. Number of flower visitors (N) to Pachycereus weberi and Pilosocereus chrysacanthus captured during the flowering period of the columnar cacti, and numbers of individuals carrying pollen of the species

Month	Leptonycteris curasoae		Leptonycteris nivalis		Choeronycteris mexicana		Stumira lilium		Artibeus jamaicensis		Artibeus intermedius		Chiroderma salvini		Glossophaga soricina	
	N	pollen	N	pollen	N	pollen	N	pollen	N	pollen	N	pollen	N	pollen	N	pollen
Pachycereus weberi																
Jan	0	0	0	0	0	0	3	1	0	0	0	0	0	0	1	1
Feb	1	1	1	1	1	1	3	1	18	6	0	0	1	0	0	0
Mar	3	3	0	0	2	2	0	0	1	0	0	0	0	0	0	0
Nov	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Dec	5	4	5	2	0	0	0	0	2	1	0	0	0	0	0	0
Total	10	8	6	3	3	3	6	2	23	7	1	0	1	0	1	1
Pilosocereus chrysacanrhus																
Mar	0	0	0	0	0	0	0	0								
Apr	10	7	2	2	2	2	1	1								
May	1	1	2	1	1	1	0	0								
June	0	0	0	0	1	1	1	1								
Total	11	8	4	3	4	4	2	2								

of floral visitors rob nectar and only one is capable of fertilization (Koptur, 1984; Webb, 1984; Petanidon & Vogel, 1993).

Although bats are scarce during winter, they are present where flower resources are available. Therefore, it seems that some nectarivorous bats stay all year round and forage in the dry woodland of the Tehuacán Valley and later in the arid scrub. Four species of nectar feeding bats (*Leptonycteris curasoae, L. nivalis, G. soricina* and *Choeronycteris mexicana*) and two frugivorous bats (*Artibeus jamaicensis* and *Sturnira lilium*) were most common visiting flowers of *Pachycereus weberi*. In the case of *Pilosocereus chrysacanthus*, flowers are visited by *L. curasoae, L. nivalis* and *C. mexicana* and only by one frugivorous bat, *S. lilium*. Considering the low frequency and abundance of pollen found on the bodies of the frugivorous species, it is possible that only nectar-feeding bats successfully pollinate these two cacti.

The probable year-round residence of nectar-feeding bats in central Mexico contrasts with the general view that nectarivorous bats (specially *Leptonycteris curasoae, L. nivalis* and *C. mexicana*) migrate to the south during winter (Howell, 1979; Humphrey & Bonaccorso, 1979; Koopman, 1981; Cockrum, 1991). In the Tehuacán Valley, nectar-feeding bats are abundant from April to July when most of the columnar cacti are flowering and fruiting (Valiente-Banuet *et al.*, 1996) and they probably move altitudinally to the nearby deciduous forests during winter (Rojas, 1996) leaving many individuals static throughout the year. If the bats are moving altitudinally, *Pachycereus weberi* is an important resource because it is a dominant species in the southern part of the Tehuacán Valley and in the Balsas River Basin. The possible year-round residence of nectarivorous bats has been also reported by Fleming *et al.* (1993) for Baja California.

Pachycereus weberi and *Pilosocereus chrysacanthus* flower when there are apparently few pollinators. However, all the flowers monitored in this study produced mature fruits. These two cacti species occur in low densities when compared to the 1200 individuals per ha reported for *Neobuxbaumia tetetzo* (Valiente-Banuet & Ezcurra, 1991) which blooms in the central part of the Valley in April and May, and when compared to the 1800 individuals per ha of *Neobuxbaumia mezcalaensis* (H. Brav. Holl.) Backeb. and *N. macrocephala* (F.A.C. Weber) Dawson which grow together in the western part of the Valley (Valiente-Banuet *et al.*, in press). The spatial distribution of *Pilosocereus chrysacanthus* may control long distance flight of bats forcing, therefore, high levels of outcrossing (Koptur, 1984; Zimmerman, 1988). A possible response to winter scarcity of pollinators is the long blooming period found in these two plant species. The flowering season lasted 5 months in *Pachycereus weberi* whose average flower production per adult during 3 nights was 4·8 flowers (S.D. = 3·6; $N = 10$ plants), and between 3 and 5 months for *Pilosocereus chrysacanthus* at an average of 2·3 flowers per plant per night (S.D. = 1·41; $N = 10$ plants). This contrasts with the 2-month flowering period for *Neobuxbaumia tetetzo, N. macrocephala* and *N. mezcalaensis* (Valiente-Banuet *et al.*, 1996, in press). The long blooming periods found in the two cacti species studied, and possibly its variation in *Pilosocereus chrysacanthus*, is a way of ensuring fruit production in conditions of pollinator scarcity (Weiner, 1988; Copland & Whelan, 1989; Wolf & Stiles, 1989; Calvo & Horvitz, 1990).

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