

GEOGRAPHIC DIFFERENTIATION IN THE POLLINATION SYSTEM OF THE COLUMNAR CACTUS *PACHYCEREUS PECTEN-ABORIGINUM*¹

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The pollination biology of the cactus *Pachycereus pecten-aboriginum* was studied in a tropical location in western Mexico (ca. 18° N latitude) to compare with data from a northern population (ca. 28° N latitude). Throughout this range, the nectar-feeding bat *Leptonycteris curasoae* is resident within the tropics but migratory in its northern range. The hypothesis was tested that if a predictable bat presence has been an important force in the evolution of pollination systems in columnar cacti, *P. pecten-aboriginum* will have a specialized pollination system within the tropics and a generalized pollination system in northern populations. In both areas, pollination experiments showed that *P. pecten-aboriginum* has a self-incompatible, hermaphroditic breeding system. In the tropical area, flowers open at night and close early in the morning. Nectar is secreted only during the night, and flowers are exclusively pollinated by three species of nectar-feeding bats, indicating a specialized pollination system. In contrast, anthesis and nectar secretion in northern populations occur during the night and day, allowing visitation and effective pollination by both nocturnal and diurnal pollinators. This study provides evidence of divergence mediated by pollinator predictability (resident vs. migrant), through shifts from short to long anthesis and nectar production periods from southern to northern populations.

Key words: Chamela region; columnar cacti; generalization; *Leptonycteris curasoae*; *Pachycereus pecten-aboriginum*; pollination biology; Sonoran desert; specialization.

In the last decade, columnar cacti (tribe Pachycereeae) have been considered to be an ideal system for exploring the causes of evolution of specialized vs. generalized pollination systems (Valiente-Banuet et al., 1996; Fleming et al., 2001). This group of plants relies heavily on animals for pollination services and of 70 species found in Mexico, 72% exhibit a bat-pollination syndrome (Valiente-Banuet et al., 1996, 2002). The geographic distribution of these plants overlaps with the distribution of the nectar-feeding bats in North America, with the center of diversity of both columnar cacti and bats being south-central Mexico (Valiente-Banuet et al., 2002). Pollination exclusion experiments conducted within and outside the tropics have revealed a clear geographical pattern in which columnar cacti show specialized pollination within the tropics, where they are highly dependent on nectar-feeding bats (Valiente-Banuet et al., 1996, 1997a, b; Nassar et al., 1997), and generalized pollination outside the tropics, where they are pollinated by a variety of animals, including birds, bats, and insects (Alcorn et al., 1961, 1962; Fleming et al., 1996, 2001). Valiente-Ban-

uet et al. (1996, 1997a) suggested that this geographical pattern reflects year-to-year variation in the abundance and reliability of the nectar-feeding bat *Leptonycteris curasoae* Martínez & Villa (Phyllostomidae, Glossophaginae), the most important nocturnal pollinator of columnar cacti in the Tehuacán Valley (Valiente-Banuet et al., 1996, 1997a, b) and the Sonoran desert (Fleming et al., 1996, 2001). Capture records of *Leptonycteris curasoae* in North American mammal collections (Rojas-Martínez et al., 1999) indicated that this bat may be resident year-round in the tropics (at latitudes below 21° N) where resources are available throughout the year, but migratory in extratropical deserts (at latitudes above 28° N) where resources are seasonally available, forcing bats to move towards the tropical deciduous forests of southern Sonora and Sinaloa.

The evidence on geographic divergence in the pollination systems comes mainly from comparisons among species of columnar cacti living in tropical and extra-tropical deserts (Fleming et al., 1996, 2001; Valiente-Banuet et al., 1996, 2002). Comparative data indicate that the shift from specialized to generalized systems has not involved major changes in flower morphology but rather subtle changes in the timing of flower closing. Columnar cacti from the Sonoran desert have flowers that remain open for 19–23 h and secrete nectar during the night and day, whereas in the Tehuacán Valley, flowers remain open for 12–15 h and secrete nectar mainly at night (Fleming et al., 1996, 2001; Valiente-Banuet et al., 1996,

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2002). Although a geographic comparison among species has revealed interesting trends, little insight has been gained about the mechanism underlying the transition from specialized to generalized systems. Our knowledge about the phylogeny of columnar cacti is limited (Terrazas and Loza-Cornejo, 2002; Wallace, 2002), and consequently, it is difficult to map the evolutionary transition (Sakai and Weller, 1999) from specialized to generalized pollination systems on a phylogenetic tree. An ideal plant system to study the mechanism underlying the evolution of pollination systems of columnar cacti would be a widespread species distributed from areas where bats are resident and reliable to areas where bats are migratory and unreliable. This appears to be the case of *Pachycereus pecten-aboriginum* (Engelm) Britton & Rose, which has probably the widest distribution among Mexican columnar cacti. It is distributed from the Isthmus of Tehuantepec (ca. 16° N) in the state of Oaxaca (Bravo-Hollis, 1978) to east-central Sonora (ca. 29° N) and southern Baja California (Turner et al., 1995). Most of its southern range is within the range in which *L. curasoae* is resident, whereas its northern range is within the range in which *L. curasoae* is migratory (Rojas-Martínez et al., 1999). Northern populations of *P. pecten-aboriginum* have flowers that open at night but remain open during the day, allowing visitation by both nocturnal and diurnal visitors (Molina-Freaner et al., 2004). Pollination exclusion experiments have shown that the contribution of nocturnal pollinators is low, whereas diurnal visitors are the most important pollinators (Molina-Freaner et al., 2004), indicating that northern populations have a generalized pollination system that resembles the pollination system of columnar cacti from the Sonoran desert. However, no information has been reported on the pollination system of southern populations of *P. pecten-aboriginum*.

In this paper, we study the pollination system of *Pachycereus pecten-aboriginum* at a southern population (18° N latitude), where the nectar-feeding bat *L. curasoae* is resident (Rojas-Martínez et al., 1999; Stoner et al., 2003), to compare our results with those reported for northern populations (Molina-Freaner et al., 2004), where *L. curasoae* is migratory (Rojas-Martínez et al., 1999). Models of the evolution of pollination systems predict specialization wherever pollinators are predictably available in space and time and generalization wherever pollinators are unpredictable (Waser et al., 1996). Therefore, this study was designed to test the hypothesis that if the abundance and predictability of *L. curasoae* have been important forces in the evolution of pollination systems in columnar cacti (Valiente-Banuet et al., 1996), we would expect to find a specialized pollination system in southern populations of *Pachycereus pecten-aboriginum*. Accordingly, we expected that, rather than major changes in flower morphology, this pattern would be reflected in (1) changes in the timing of flower closing, with a shorter period in southern populations, (2) changes in duration of nectar secretion, with secretion only at night in southern populations, but both nocturnal and diurnal secretion in northern populations, and (3) changes in the duration of stigma receptivity, with longer receptivity in northern populations than in the southern ones. It is unknown if the shift in the pollination systems of columnar cacti has involved changes in the sugar composition in floral rewards (Baker and Baker, 1983). However, nectar in specialized bat pollination systems should be characteristically dominated by monosaccharides, while a generalized pollination system (for attracting birds, bats, and insects) should have nectar composed mainly

of disaccharides (Baker and Baker, 1983). Therefore, in this study we compare the sugar composition (sucrose, glucose, and fructose) in the nectar of southern vs. northern populations.

MATERIALS AND METHODS

Study site—We studied a population of *P. pecten-aboriginum* at Isla Pajarera, an island located in the Chamela bay, in the state of Jalisco, Mexico, during 19–27 March 1998 and 27 February–16 March 2002 (Fig. 1). Isla Pajarera is ca. 2 km from the coast (19°30' N; 105°03' W). Vegetation on the island is a tropical deciduous forest (Lott, 1985) in which *P. pecten-aboriginum* is a structural dominant species. Other common species are *Cordia alliodora* (Ruiz & Pavón) Oken, *C. eleagnoides* DC, *Crataeva tapia* L., *Caesalpinia eriostachys* Benth., *Acanthocereus occidentalis* Britton & Rose, and *Stenocereus standleyi* González Ortega. Annual precipitation averages 733 mm (1977–1983), 81% of which falls between July and November (Lott, 1985). Temperature ranges from 16°C in January to 31°C in July. During our work in February 1998, weather was temperate with minimum night temperatures of 16°C and maximum day temperatures of 27°C. During this period, an exceptional storm with nearly 30 mm of rain (Ayala, Instituto de Biología, Universidad Nacional Autónoma de México [UNAM]) caused a massive elimination of flowers of *P. pecten-aboriginum* and, therefore, a second period of field work, from 27 February to 2 March and from 14 to 16 March 2002 was necessary. In this period, minimum night temperature was 18°C, maximum day temperature was 31°C, and no rain occurred.

Plant abundance, flowering intensity, and flower availability—Density of *P. pecten-aboriginum* was estimated by counting the number of juvenile and adult plants in two 40 × 16 m² plots and one 40 × 12 m² plot. We measured the height of the major axis and number of branches on each plant. We defined flowering intensity as the frequency of flowering individuals in a sample of 29 multibranching plants on 23 March 1998, 27 February 2002, and 14 March 2002. Number of open flowers per adult for a sample of 29 multibranching plants was counted during three consecutive nights when pollination treatments were applied (see next section) to estimate resource availability for pollinators.

Floral biology—The dimensions of one flower from each of 29 plants were measured. Measurements included flower length (i.e., from petal tip to flower base), external diameter at the corolla apex, and internal diameter of floral tube at the point of anther dehiscence. We also used this sample to verify if flowers were hermaphrodite (i.e., we checked ovaries for presence of ovules and anthers for pollen). To describe flower opening and closure, we measured the distance between opposite tepal tips in a sample of 12 flowers from 12 plants every 2 h, starting at bud opening. Flower receptivity was recorded by monitoring anther dehiscence and stigma turgidity in 10 flowers from 10 plants every 2 h. Nectar volume secreted by flowers was measured from opening to closure of flowers in a sample of 19 bagged flowers from nine plants. Nectar was extracted every 2 h using a graduated milliliter syringe and not replaced. Flowers were bagged before anthesis with netting and were kept bagged after each measurement. Sucrose concentration was also measured every 2 h with a handheld refractometer (ERMA Brix/ATC 113, St. Louis, Missouri, USA). For each measurement, a sample of nectar was collected in a separate vial per flower. Thus, total nectar production per flower was sampled separately ($N = 13$) and maintained on ice until laboratory analyses for sucrose, glucose, and fructose content using a medium infrared analyzer as described by Flores-Ortiz et al. (2003). Nectar from a northern population of *P. pecten-aboriginum* collected by Molina-Freaner et al. (2004) during 1998 was analyzed in the same way. We compared the concentration of each sugar with a Student's *t* test assuming no significant differences among sugar types in flowers among localities.

One about-to-open flower was collected from 10 plants and preserved in 70% ethanol to count ovules in the laboratory, and the average number of ovules was used for further analyses of seed set.

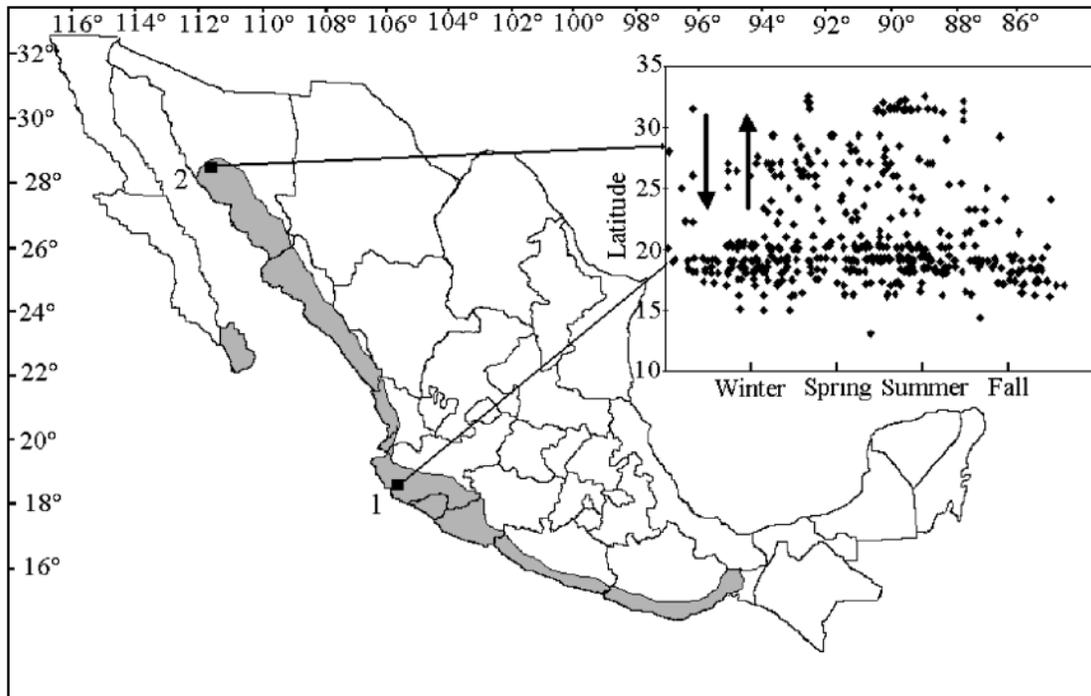


Fig. 1. Range of distribution and location of the studied population of *Pachycereus pecten-aboriginum* at Isla Pajarera in Mexico (1) in the state of Jalisco and the Sonoran population (2, studied by Molina-Freaner et al., 2004). Inset graph shows the location of 94-yr capture records of *Leptonycteris curasoae* with respect to latitude and season. Arrows indicate the proposed migratory movements of this bat at its northern range and continuous presence at ca. 18° N latitude (modified from Rojas-Martínez et al., 1999).

Breeding system—To determine whether flowers are self-compatible and nocturnal and diurnal visitors are effective, we conducted pollination experiments on a total of 189 tagged flowers in six pollination treatments across 29 plants. Different numbers of flowers were assigned to each of the following treatments: (1) autonomous self-pollination ($n = 35$ flowers on 10 plants), in which buds were bagged with netting and left without manipulation until flowers closed; (2) manual self-pollination ($n = 30$ on 10 plants), in which flower buds were bagged, flowers hand-pollinated soon after the flowers opened with pollen from the same flower; (3) nocturnal pollination ($n = 32$ on 16 plants), in which flower buds were tagged before opening and were exposed to nocturnal visitors during night and excluded from diurnal visitors by bagging flowers at sunrise; (4) diurnal pollination ($n = 30$ on 12 plants), in which flower buds were bagged and remained unavailable to nocturnal visitors, then flowers were exposed to diurnal visitors by removing the bag at sunrise until the flowers closed; (5) manual cross-pollination treatment ($n = 33$ on 10 plants), in which flower buds were bagged, and when flowers opened they were hand-pollinated by saturating the stigma with fresh pollen obtained from another plant; (6) open-pollinated control ($n = 29$ on 20 plants), in which flowers that opened during three consecutive days were tagged, and these flowers were available to nocturnal and diurnal visitors. The fate (aborted or developing fruit) of the tagged flowers from pollination treatments was scored. Fruits were monitored every month until they matured. Mature fruits were collected in mid-June. Seeds were directly counted from the collected fruits and compared with the average number of ovules to calculate seed set.

Fruit set and number of seeds per fruit among pollination treatments were analyzed by logistic models. Number of seeds among treatments was analyzed by a one-way ANOVA. All statistical analyses used JMP 3.1 software (Sall and Lehman, 1996, SAS Institute).

Flower visitors—Nocturnal and diurnal visitors were identified by placing 10 mist nets (10 m long \times 2 m tall, separated by \approx 100 m) during 3 d across an area with a high density of *P. pecten-aboriginum*. For each animal caught, pollen preparations were made by rubbing a cube of fuchsin-stained jelly

(Beattie, 1971) over the animal'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. Pollen grains from animal samples were later compared with those obtained directly from flowers of *P. pecten-aboriginum*.

Nocturnal vs. diurnal effectiveness—Values of nocturnal and diurnal effectiveness of pollination were calculated by multiplying the relative abundance of pollinators, the frequency of pollen presence in nocturnal or diurnal visitors, and nocturnal or diurnal seed set. These values were calculated similarly to those for the northern population studied by Molina-Freaner et al. (2004). Seed set values for this population were obtained by counting ovules produced by 25 flowers from 25 different plants.

RESULTS

Plant abundance, flowering intensity, and flower availability—Mean density of *P. pecten-aboriginum* was 338.5 ± 80 plants/ha (mean \pm 1 SE) but density of reproductive individuals (>2 m tall) was 229 ± 36.4 adults/ha. Adult plants reach heights of 6–7 m and 45–47 fertile branches (>1 m). Flowering intensity was moderately high during the pollination treatments (0.73 during 20–22 March 1998, 0.79 during 27 February–2 March 2002, and 0.82 during 14–15 March 2002). During the three consecutive nights pollination treatments were applied, adult (multibranched) individuals produced 2.49 ± 1.89 to 4.63 ± 3.48 flowers/plant (range 1–11 flowers/plant).

Floral biology—All dissected flowers at Isla Pajarera were hermaphrodites, started to open at dusk (ca. 1900 h), began to close at 0700 and flowered for 12.2 ± 0.34 h (mean \pm 1 SE). Nectar production was continuous only during anthesis until

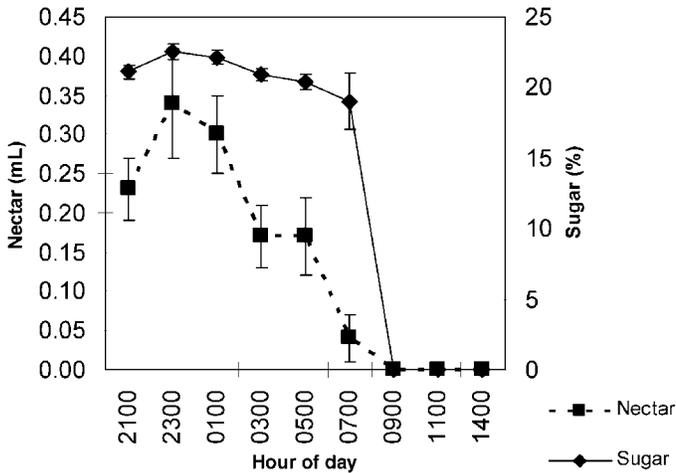


Fig. 2. Temporal course of nectar production and sugar concentration in flowers of *Pachycereus pecten-aboriginum* at Isla Pajarera, Chamela Jalisco. Bars indicate one standard deviation.

0730 (Fig. 2), and no evidence was found of diurnal nectar production. Comparative data (Table 1) indicate that anthesis duration in the northern population was 20.5 ± 1.23 h with diurnal nectar production. Likewise, flower dimensions and the number of ovules per flower of *P. pecten-aboriginum* were similar between populations. Only perianth width was larger at Isla Pajarera than in Sonora ($t = 38.23$; $df = 55$; $P < 0.001$; Table 1). Concentration of sucrose ranged from 16.6 to 22.3% in Sonora and from 20.3 to 22.5% at Isla Pajarera (Fig. 2). Sugar composition was similar between localities; nectar from both sites was rich in monosaccharides (see Table 1).

Breeding system—No fruit was set by any flowers of *P. pecten-aboriginum* that were hand self-pollinated and excluded from visitors (Table 2). Fruit set ranged from 44% in the manual cross pollinations to 55% in open-pollinated controls (Table 2). Nocturnal visitors produced a similar fruit set (56%), whereas diurnal visitation produced no fruit. Differences between control and cross-pollination treatments were not significant ($\chi^2 = 0.229$; $df = 1$; $P = 0.63$), as well as fruit set produced by nocturnal pollination and manual out-crossed plants ($\chi^2 = 0.763$; $df = 1$; $P = 0.3821$).

Mean number of seeds per fruit ranged from 489 in the nocturnal treatment to 650.6 in the control (Table 2). Differences between control, cross-pollination, and nocturnal-pollination treatments were significant for seed set ($\chi^2 = 7.71$; df

$= 2$; $P = 0.02$). Seed set ranged from 57% in the nocturnal pollination, 58% in manual cross pollination to 76% in the open-pollinated control (Table 2).

Flower visitors—During 1998, 83 individuals of the bat *Leptonycteris curasoae* and four of *Choeroniscus godmani* Thomas were caught at Isla Pajarera; all these bats bore pollen of *P. pecten-aboriginum*. During the 2002 field work, when the pollination experiments were repeated, 18 individuals of *L. curasoae* and four of *Glossophaga soricina* Pallas were caught, all of them bearing pollen of *P. pecten-aboriginum*. No diurnal visitors were caught and only individuals of the bee *Apis mellifera* L. were observed visiting flowers.

Nocturnal vs. diurnal effectiveness—Pollination-effectiveness values for nocturnal pollinators in Sonora and Isla Pajarera were 0.0042 and 0.48, respectively, but 0.159 and 0, respectively, for diurnal pollinators.

DISCUSSION

This study provides direct evidence of geographic variation in the pollination system of a columnar cactus that is clearly linked to pollinator predictability. Our data show that population dynamics of pollinators (resident vs. migrant nectar-feeding bats) have an important influence on the pollination system. Our evidence supports the ideas stated by authors such as Waser et al. (1996), Gómez and Zamora (1999), and Johnson and Steiner (2000), predicting generalization provided that temporal and spatial variance in pollinator quality and identity are appreciable. The contrasting conditions of pollinator predictability have an important effect on anthesis time, nectar secretion, and stigma receptivity, with longer periods in northern populations. Morphological differentiation was restricted to perianth width, but such a difference might be associated with the type of pollinator or to resource limitation as has been discussed by Pellmyr and Thompson (1996).

Both populations had a self-incompatible, hermaphroditic breeding system and floral rewards (nectar) rich in monosaccharides, a pattern corresponding to a chiropterophilous pollination syndrome (Faegri and van der Pijl, 1979; Baker and Baker, 1983), suggesting that bats were the main pollinators of cacti ancestors of both populations. Pollination experiments in the northern populations showed a nocturnal fruit set of 0.04 given by a strong scarcity of bats, whereas diurnal pollination resulted in a fruit set of 0.18, indicating that diurnal pollinators are more important than nocturnal pollinators (Molina-Freaner et al., 2004). The relative importance of nocturnal and diurnal

TABLE 1. Floral biology and nectar composition of *Pachycereus pecten-arboriginum* at Isla Pajarera and in the Sonoran population studied by Molina-Freaner et al. (2004). Data are means \pm 1 SE. An asterisk indicates significance.

Floral trait	Sonora	Isla Pajarera	Significance		
			t	df	P
Total length (cm)	7.53 \pm 0.18	7.55 \pm 0.17	0.653	55	>0.20
Perianth width (cm)	2.63 \pm 0.06	2.76 \pm 0.05	38.23	55	<0.001*
Ovules per flower (n = 10)	704.9 \pm 45.7	854.7 \pm 90.8	0.27	30	>0.2
Anthesis duration (h)	20.5 \pm 1.23	12.2 \pm 0.34	21.9	26	<0.0001*
Nectar concentration during night (sucrose units)	20.18 \pm 0.82	21.0 \pm 0.52	1.98	28	>0.20
Nocturnal nectar production (mL)	0.69 \pm 0.02	1.25 \pm 0.04	478.6	28	<0.001*
Diurnal nectar production (mL)	0.13 \pm 0.05	0	104	6	<0.001*
Total fructose	7.45 \pm 0.75	7.51 \pm 0.61	0.128	12	>0.20
Total glucose	7.82 \pm 0.79	9.14 \pm 0.16	0.324	12	>0.20
Total sucrose	4.59 \pm 1.44	3.28 \pm 0.61	1.22	12	>0.20

TABLE 2. Fruit set, seed set, number of flowers, and number of seeds per fruit in different pollination treatments of *Pachycereus pecten-aboriginum* at Isla Pajarera, Chamela. Seed set values calculated for the Sonoran population studied by Molina-Freaner et al. (2004) are also given. Values are means with standard errors in parentheses.

Pollination treatment	Isla Pajarera					Sonora Seed set
	Fruit set	No. plants	No. flowers	No. seeds/fruit	No. fruits	
Autonomous self-pollination	0	10	35	0	0	0
Manual self-pollination	0	10	30	0	0	0
Diurnal pollination	0	12	30	0	0	0.17 (0.05)
Nocturnal pollination	0.56 (0.12)	16	32	489.63 (43.85)	22	0.14 (0.0)
Open pollinated control	0.55 (0.16)	20	29	650.6 (52.27)	20	0.33 (0.04)
Manual cross-pollination	0.44 (0.11)	10	33	503.5 (27.92)	17	0.61 (0.07)

pollinators thus varies in space and time and, when pollen has been limited, the “missing” pollinator has been *L. curasoae* (Fleming et al., 1996, 2001; Molina-Freaner et al., 2004). In Sonora, *L. curasoae* was rare and likely to be the “missing” pollinator responsible for the low fruit set and lower number of seeds per fruit observed in open-pollinated flowers of *P. pecten-aboriginum*. Flowers were open and receptive during the day, and several bird species, such as *Melanerpes uropygialis* Baird, *Colaptes auratus* L., and the finch *Carpodacus mexicanus* S. Muller, were observed placing their heads in flowers and touching stigmas. The lower numbers of seeds per fruit and seed set in flowers exposed to diurnal visitors in the Sonoran desert probably reflect lower pollen loads and reveal that these opportunistic pollinators are not as effective as nectar-feeding bats (Molina-Freaner et al., 2004). Thus, the pollination biology of northern populations of *P. pecten-aboriginum* resembles the generalist pollination system of columnar cacti from the Sonoran desert (Fleming et al., 1996, 2001), in which flowers have the longest anthesis (19–23 h) than any other columnar cacti in the tropics (Valiente-Banuet et al., 2002). A similar pattern has been reported for *Agave palmeri* Engelm. and *A. chrysantha* Peebles (Agavaceae), which have several chiropterophilous traits, but are pollinated during the day and night by a wide diversity of pollinators at their northern range in the Sonoran desert (Slauson, 2000). In all cases, the pattern of nocturnal/diurnal nectar production and stigma receptivity promote both nocturnal and diurnal pollination. Likewise, the long anthesis periods found in extra-tropical populations seem to be related to some degree to temperature and humidity, similar to that reported for the cactus *Lophocereus schottii* (Engelman) Britton & Rose (Fleming and Holland, 1998), or even within the tropics, as has been reported for *Pachycereus weberi* (J.M. Coulteri) Backeb. and *Polaskia chichipe* (Gosselin) Backeberg, whose maximum anthesis period may reach more than 20 h during cold winters when pollinators are scarce (Valiente-Banuet et al., 1997b; Otero-Arnaiz et al., 2003). Thus, the evolution of the generalist pollination systems in non-tropic climates may have evolved through phenotypic response related to climatic conditions, which in turn may affect pollinator activity.

On the other hand, at Isla Pajarera no evidence of pollination limitation by bats was found. Nocturnal pollinators were the unique effective visitors that produced statistically the same fruit and seed set as the manual cross-pollination treatment and control. Beside the bat *L. curasoae*, which undoubtedly is the most abundant, two other species, *Glossophaga soricina* and *Choeronycteris godmani*, were caught carrying pollen of *P. pecten-aboriginum*. The pollination system in this tropical population of *P. pecten-aboriginum* resembles the specialized pollination systems of columnar cacti documented for

south-central Mexico and Venezuela (Valiente-Banuet et al., 1996, 1997a, b; Nassar et al., 1997) and is characterized by a complete dependence on the nectar-feeding bats (*Leptonycteris curasoae*, *L. nivalis* Saussure, and *Choeronycteris mexicana* Tshudi) that are reported as specialized pollen and nectar consumers (Alvarez and González, 1970; Cockrum, 1991; Valiente-Banuet et al., 1996, 1997a, b). Similar to nectar-feeding bats of south-central Mexico that move altitudinally rather than latitudinally to find floral food resources throughout the year (Rojas-Martínez et al., 1999), nectar-feeding bats in the area of Isla Pajarera maintain roosts all year round, moving locally to search for feeding resources (Stoner et al., 2003).

In summary, the spatial-temporal unpredictability of nectar-feeding bats, which are the most important pollinators of most columnar cacti, is the most important factor that is likely to exert selection pressures on floral traits by pollinators in extra-tropical deserts. This mechanism may explain the evolution of the generalist pollination system outside the tropics vs. a specialized bat-pollination system within the tropics in *Pachycereus pecten-aboriginum*. This hypothesis might also explain the dichotomy reported within vs. outside the tropics for other columnar cacti showing a chiropterophilous pollination syndrome.

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