DIVERSITY OF FLORAL VISITORS TO *ECHINOPSIS ATACAMENSIS* SUBSP. *PASACANA* (CACTACEAE)

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Abstract: Columnar cacti can be pollinated by various insect and vertebrate species, often showing either close adaptations to a single pollinator group, or a mixed pollination syndrome, depending on a variety of different animals for pollination. As pollination data for columnar cacti in South America are scarce, we investigated the spectrum, frequency, and behavior of floral visitors in *Echinopsis atacamensis* subsp. *pasacana*. We compared two habitats with differences in mean annual precipitation and human impact, finding considerably higher activity and diversity of flower visitors in the population with higher humidity. Bees, wasps, and the giant hummingbird (*Patagona gigas*) were shown to visit cactus flowers during the day to gather nectar or pollen. We found marked differences in the spectrum of floral visitors between both populations. In one study site, the introduced honeybee *Apis mellifera* removed large quantities of pollen, but seemed to be a comparatively inefficient pollinator. Additionally, first evidence for visits by nocturnal hawkmoths is provided. These results demonstrate an unspecialized floral syndrome for *Echinopsis atacamensis* subsp. *pasacana*, with both diurnal and nocturnal pollinators. Such a mixed floral syndrome is fairly widespread among columnar cacti in the northern hemisphere but was hitherto only shown for one South American species, *Weberbauerocereus weberbaueri*.

Key words: Argentina, bees, Cactaceae, columnar cacti, *Echinopsis atacamensis* subsp. *pasacana,* giant hummingbird, *Patagona gigas*, pollination biology

Introduction

Columnar cacti are among the most conspicuous plants in New World arid environments. Since they are crucial for the survival of many other organisms, providing them with resources and shelter, they have been the subject of many ecological studies, including investigations on their pollination biology. However, most of the work on pollination biology in columnar cacti has been done on North, Central, and northern South American species (Fleming and Valiente-Banuet, 2002). In the inner tropics, flowers of most columnar cacti are predominantly nocturnal and often exclusively pollinated by bats (Valiente-Banuet et al., 1996; Nassar et al., 1997). A highly specific pollinator-plant relationship is found in southern North America, with obligate mutualism between *Pachycereus schottii* (Engelmann) D. R. Hunt and the moth *Upiga virescens* Hulst (Lepidoptera, Pyralidae) that actively pollinates the flowers before laying its eggs on them (Fleming and Holland, 1998 [as *Lophocereus schottii*]). Further, pollination by hawkmoths (Silva and Sazima, 1995; Valiente-Banuet et al., 1996), as well as specialization for hummingbird pollination (Gibson and Horak, 1978; Valiente-Banuet et al., 1996) has been reported. Adaptation to bee pollination is comparatively rare in columnar cacti (Valiente-Banuet et al., 2002). Mixed pollination, resulting from different proportions of bats, birds and bees as pollinators, was reported for different species of columnar cacti. This pollination syndrome seems to replace bat pollination in the outer tropics (Nassar et al., 1997). In northern Mexico and the southern United States, this mixed pollination was reported for *Carnegiea gigantea* (Engelmann) Britton & Rose, *Pachycereus pringlei* (S. Watson) Britton & Rose and *Stenocereus thurberi* (Engelmann) Buxbaum (McGregor et al., 1962; Fleming et al., 1996, 1998; Valiente-Banuet et al., 2002). In South America, similar observations have only

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been made for *Weberbauerocereus weberbaueri* (K. Schumann ex Vaupel) Backeberg (Sahley, 1996) in southwestern Peru.

Most abundant in the central Andes are columnar cacti belonging to the genus *Echinopsis* (formerly treated as *Trichocereus*). About 25 species can be considered columnar, growing up to 12 m tall (Anderson, 2001). Among them, *Echinopsis atacamensis* (Philippi) H. Friedrich & G. D. Rowley subsp. *pasacana* (F. A. C. Weber ex Rümpler) G. Navarro (=*Trichocereus pasacana*) is widespread in the arid to semiarid prepuna in northwestern Argentina and southeastern Bolivia, forming large cactus forests (Kiesling, 1978). Badano and Schlumberger (2001) observed that flowers of *E. atacamensis* subsp. *pasacana* are xenogamous, therefore depending on animals to promote outcrossing. The white-pinkish flowers open in the evening and remain open during the next day (de Viana et al., 2001). These studies also showed that nectar production was highest at night but only diurnal bees were reported to visit the flowers. Nearly a century ago, hummingbird visits were also observed for *E. atacamensis* subsp. *pasacana* (Fries, 1903, cited in Porsch, 1939).

According to these previous observations and floral morphology, we hypothesized that flowers of *E. atacamensis* subsp. *pasacana* are visited by a variety of animals, both diurnal and nocturnal, showing a similarly broad visitor spectrum as some other columnar cacti in the outer tropics of North America and southern Peru. We collected data on the spectrum of floral visitors to *E. atacamensis* subsp. *pasacana* and their relative frequency and behavior during a limited time period within the main flowering season. We compared two cactus populations in ecologically distinct habitats, contrasting the presence/absence of the introduced honeybee *Apis mellifera*. Because former reports indicated bee pollination for *E. atacamensis* subsp. *pasacana*, we studied the frequency of flower visitation of different Hymenoptera species and compared these findings with differences in reproductive success of these cacti reported earlier for the same locations (Badano and Schlumberger, 2001). We further wanted to corroborate the old report of hummingbird visits and, as the flowers open at dusk and nectar secretion peaks at night (de Viana et al., 2001), we also checked for nocturnal visitors (the first study to do this).

Materials and Methods

Study area and period

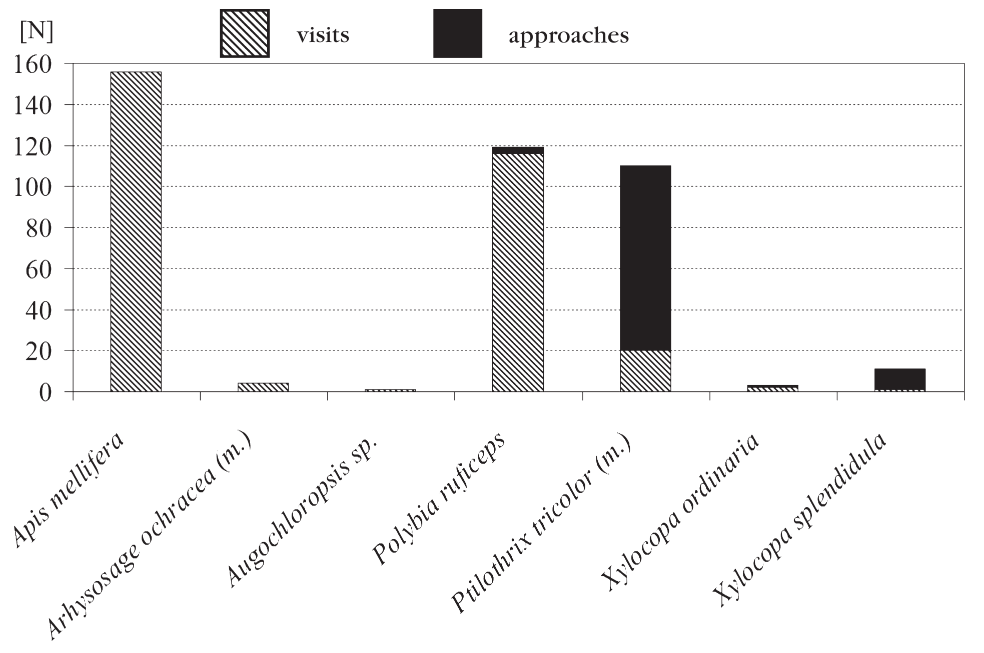
The study was carried out in two arid habitats near Cachi in the province of Salta, Argentina. The first study site (Site 1) was located between Cachi and Las Pailas (25°05′S, 66°11′W, ca. 2300 m above sea level) in close vicinity to an agricultural area with beekeeping activity. The second study site (Site 2) was located in the Tin Tin Valley (25°10′S, 66°58′W, ca. 2800 m above sea level), a natural environment without recent human influence, situated within the Los Cardones National Park. At both study sites, observations were made in a 10,000 m^2 plot. Mean annual precipitation is 146 mm at Site 1, and 90 mm at Site 2 (information provided by National Park Services, Salta). As a result of higher precipitation, a nearby river, and human activity, vegetation was much richer and more diverse at Site 1. All observations were performed during the southern hemisphere spring (November–December), the main flowering period for *Echinopsis atacamensis* subsp. *pasacana*. Studies on diurnal visitors were performed in 1998 and studies on nocturnal visitors were done in 2003. During peak blooming, observations were made on consecutive days with good weather conditions. During nighttime surveys in 2003, the temperature range at Site 1 was 13.3°C–23.0°C, and 12.0°C–14.8°C at Site 2. Relative humidity at night ranged from 24%–50% at Site 1, and from 69%–92% at Site 2.

Floral visitors and pollination

The spectrum of floral visitors to *E. atacamensis* supsp. *pasacana* was evaluated for each study site over three days in 1998. For both sites, floral visitors to 10 flowers (on five and six plants respectively per site) were recorded in one-hour periods between 07:30 and 17:00 hrs. Specimens for observation were randomly chosen. During these periods, all flower-visiting insects were counted, and their behavior was observed. We recorded three reasons for flower visitation: pollen collection, nectar collection, and searching for mates (males only). The latter can be recognized by typical behavior such as observing flowers while hovering (mostly not landing), or males waiting inside flowers for females. To estimate pollination efficiency, we observed the proportion of floral visitors that contacted the stigma during a visit. As the abundance of most native hymenoptera species was low, no adequate number of animals could be caught to analyze the pollen load as a measure for flower constancy. Specimens of each visiting species were collected for later determination. Bees were determined by J. S. Moure (Universidade Federal de Curitiba, Brazil), wasps were determined by Volker Mauss (University of Bonn, Germany) and hawkmoths were identified by Marcela Moré (Universidad Nacional de Córdoba, Argentina). To control for significance of the observed differences between both study sites we used the Kruskal-Wallis test.

Hummingbird activity was observed during a single day, counting all flower visits in the entire study site.

We applied two methods to check for hawkmoths as floral visitors: A vertical sheet light trap was installed in both study sites in 2003. Traps were illuminated with two 160W MB lamps. A



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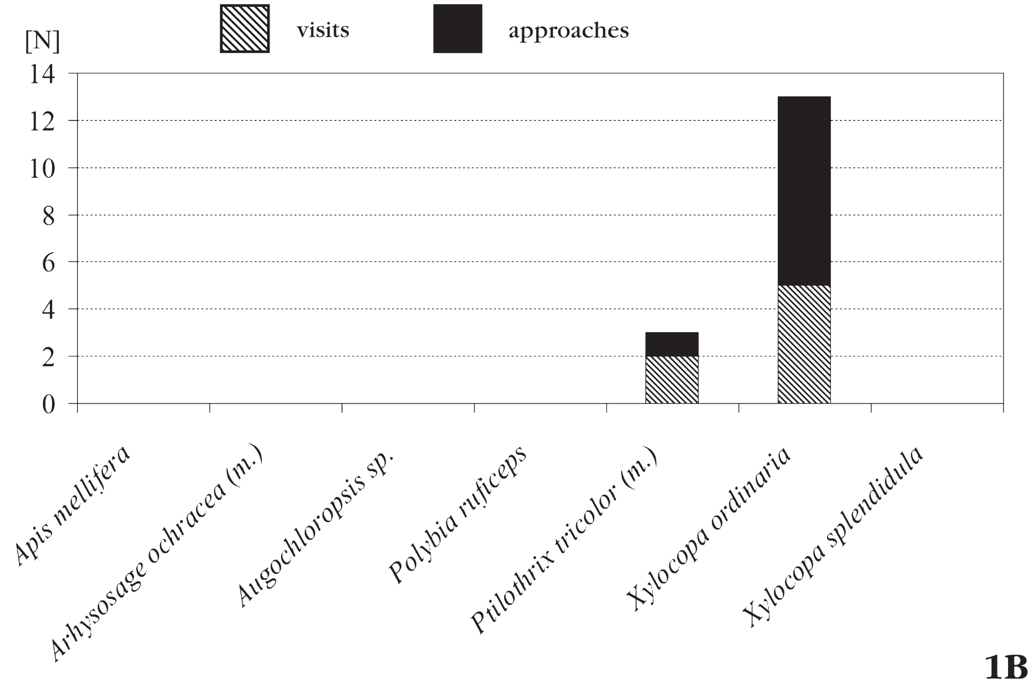

1B

Figure 1. Total number of floral visitors (including approaches without landing) on flowers of *Echinopsis atacamensis* subsp. *pasacana* during a total of 5 hours of observation (note the differences in scale). **1A.** Site 1 (Cachi-Las Pailas). **1B.** Site 2 (Tin Tin Valley).

light trap was exposed from 20:00–0:00 hrs during two nights at Site 1 and during one night at Site 2. In order to verify flower visits by *E. atacamensis* subsp. *pasacana*, the pollen load of collected hawkmoths was examined under an inverted microscope and compared with reference samples collected from flowers. Additionally, in order to provide evidence for hawkmoth visitation, stigmas of wilted flowers were collected and examined under a dissecting microscope for hawkmoth scales. Stigmas were collected from Site 1 (n = 22), Site 2 (n = 16), and additionally from specimens (n = 13) from a third population north of Humahuaca (Province of Jujuy, Argentina, 23°10′S, 65°22′W, 3080 m above sea level).

Results

Floral visitors

The flowers of *E. atacamensis* subsp. *pasacana* were mainly visited by several Hymenoptera species, i.e. solitary bees like *Arhysosage ochracea* Friese (Apoidea, Andrenidae), *Augochloropsis* sp. (Apoidea, Halictidae), *Ptilothrix tricolor* Friese (Apoidea, Anthophoridae), *Xylocopa ordinaria* Smith, and *X. splendidula* Lepeletier (both Apoidea, Anthophoridae), the non-native, social honey bee *Apis mellifera* Linnaeus (Apoidea, Apidae), and the social wasp *Polybia ruficeps* Schrottky (Vespidae, Polistinae). Queens of *Bombus opifex* Smith (Apoidea, Apidae) were seen visiting flowers at Site 1, but not encountered during the observation periods. The composition of floral visitors differed between the two study sites: both number of flower-visiting specimens and species diversity were significantly higher ($p < 0.05$ for number of bees and $p < 0.001$ for number of bee species) at Site 1 during the observation periods (Figs. 1a, b). Occasional visits by beetles and ants of undetermined species were observed at both sites. The giant hummingbird, *Patagona gigas* Vieillot (Trochilidae), was observed as a frequent flower visitor at Site 1 (Fig. 2), but was only seen on about 50% of the days. Other hummingbird species, although present in that area, were never observed to visit flowers of *E. atacamensis* subsp. *pasacana*. *Patagona gigas* was never encountered at Site 2.

Only one male specimen of the hawkmoth *Manduca diffissa* Butler (Lepidoptera, Sphingidae) was caught with the light trap at Site 1. Analysis of the carried pollen did not reveal cactus pollen. No hawkmoths were caught at Site 2. However, examination of stigmas confirmed hawkmoth visits for 2 flowers at Site 1. No hawkmoth scales were found on the stigmas collected at Site 2 and the population north of Humahuaca.

Visitor behavior

Insects visited flowers of *E. atacamensis* subsp. *pasacana* for different purposes (Fig. 3). Workers of the introduced *Apis mellifera* (81% of observed visits) and females of *Xylocopa ordinaria* (31%) predominantly visited the flowers to collect pollen, whereas workers of *Polybia ruficeps* only collected nectar. *Apis mellifera* was observed gathering pollen right after sunrise (Fig. 4) and 2–3 hours later all pollen was harvested, leading to a decrease in *Apis* activity. At Site 2, without any *Apis* present, pollen was available during the entire anthesis period. Especially in the large bees, *P. tricolor* and *X. ordinaria*, their ventral sides were covered with pollen; specimens of *X. ordinaria* usually were entirely covered with pollen of *E. atacamensis* subsp. *pasacana* (Fig. 5).

Male bees were attracted to the flowers in search of mates. All four observed males of *Arhysosage ochracea* and 20% of the observed *Ptilothrix tricolor* males landed on the flowers to search for females. Most of the *Ptilothrix* males (80%) did not land on the flower but approached flowers closely to look for females while hovering. The other insects that approached without landing (Fig. 2) were repelled either by the human observer or by insects already in the flower. In particular, specimens of both *Xylocopa* species avoided flowers occupied by *Apis mellifera*.

Frequency of stigma contact varied greatly between different species (Fig. 6). Males of *Ptilothrix tricolor* touched the stigma most frequently (95% of their visits), followed by the female *Xylocopa ordinaria* (80% of visits), both using the large stigma as a landing platform. Specimens of the remaining species touched the stigma in 50–63% of their visits.

During their harvesting flights, individuals of *Apis mellifera*, *Ptilothrix tricolor*, *Xylocopa ordinaria*, and *Polybia ruficeps* were observed visiting several flowers of *E. atacamensis* subsp. *pasacana* in a row, flying from one plant to the next.

All beetles observed visited the flowers to consume flower parts and remained in the flowers for long periods, even after flowers had wilted. Ants were observed to rob nectar by puncturing the floral tube at the base of the nectary (Fig. 7). Also, leafcutter ants dissected entire flowers.

Patagona gigas landed on the flowers to consume nectar, inserting their head, breast and abdomen in the flowers (Figs. 8, 9). The birds typically visited several flowers in a row, and were never seen to visit flowers of other species at the study site. Between flower visits, birds used the top of *E. atacamensis* subsp. *pasacana* as perches, from which they showed territorial behavior, attacking conspecific and other hummingbirds.

Discussion

Although our observations were restricted to two populations, and were performed during limited periods of time during peak blooming, the attractiveness of flowers of *E. atacamensis* subsp. *pasacana* to various invertebrate and one vertebrate species was demonstrated. For bees and

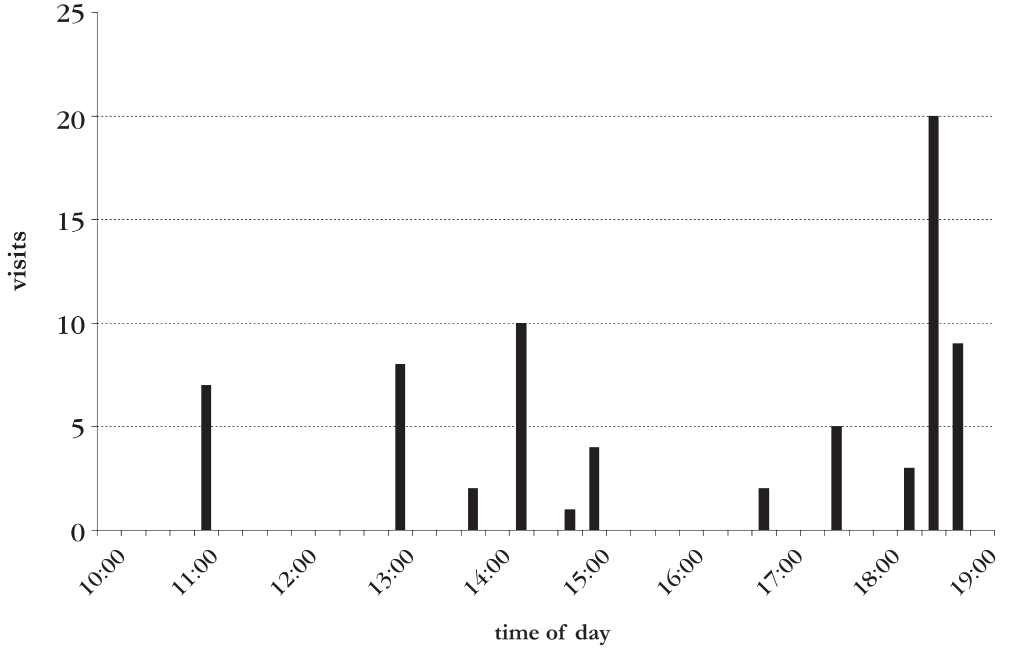

Figure 2. Flower visits of *Patagona gigas* during one day of observation at Site 1.

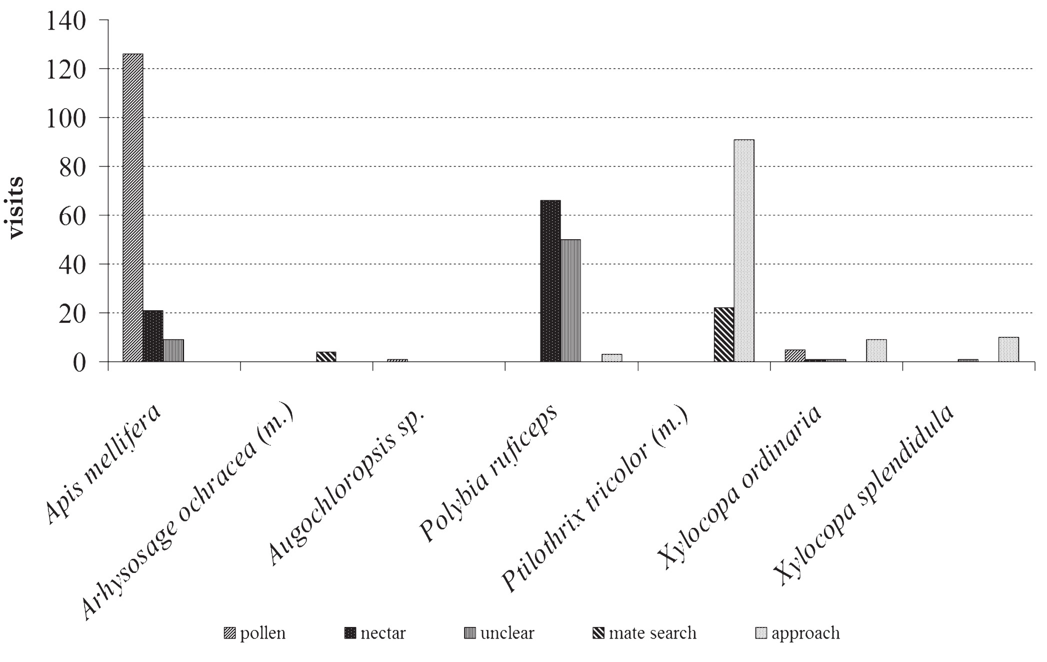

Figure 3. Frequency of observed behavior at both study sites during floral visits. Male (m) *Ptilothrix* bees mostly approached flowers in search of females. Other bees/wasps that approached without landing were most likely discouraged by the presence of the observer.

Figure 4. *Apis mellifera* transferring pollen into corbiculae (arrow) while hovering above flower of *E. atacamensis* subsp. *pasacana*. Flower = 129 mm long.

Figure 5. *Xylocopa ordinaria* covered with pollen of *E. atacamensis* subsp. *pasacana*. Bee = 23.9 mm long.

wasps the flowers provide large amounts of pollen and nectar (mean production ca. 128 µl per flower [de Viana et al., 2001]). Nectar can only be exploited by insects with a long tongue, or by insects small enough to crawl into the tube to reach the nectar. Of all insect visitors only a wasp, *Polybia ruficeps,* visited the flowers exclusively for nectar, being able to reach the nectar with their small and slender bodies. However, the elongated, tubular nectary (Fig. 7) is not fully accessible for any of the observed bee or wasp species. Nevertheless, these diurnal insects seem to play an important role as vectors for conspecific pollen, as they touch the stigmas on 50–95% of their visits.

We suggest that, among the hymenopteras, the large bees *Xylocopa ordinaria* and *Ptilothrix tricolor* are the most efficient pollinators of *E. atacamensis* subsp. *pasacana* due to their comparatively high frequency of stigma contact and the pollen being carried on the ventral side of the abdomen, especially by *Xylocopa ordinaria*. Furthermore, in almost all cases bees of both species were observed flying from one *E. atacamensis* subsp. *pasacana* plant to the next, an indication of relative flower constancy; these bees were also the only visitors that were observed at both study sites. Workers of *Apis mellifera* touched the stigmas with the lowest frequency, suggesting comparatively poor pollen transfer, which may be balanced by their high frequency at Site 1. Although the workers of *Apis mellifera* surely contribute to the overall pollination success of these cacti, their visits may have a detrimental effect caused by the heavy pollen removal and the observed deterrent effect for other visitors that may be potentially more effective pollinators.

We suspect that the observed beetles and ants do not significantly contribute to pollination of *E. atacamensis* subsp. *pasacana*. Beetles exhibited a mainly destructive behavior and remained in a single flower until after wilting, thus not showing enough mobility to contribute significantly to pollination. None of the ants observed contacted the stigma, and they are too stationary to significantly move pollen between individuals of *E. atacamensis* subsp. *pasacana*.

Although *Patagona gigas* was not seen in both study sites and not encountered during all days, it probably is an efficient pollinator of *E. atacamensis* subsp. *pasacana*. When present, these hummingbirds were shown to be frequent flower visitors, highly flower constant and defend territories that include the cacti. Their size and shape, as well as their way of entering flowers, indicates that they take up pollen with their breast and upper abdomen, and touch the stigma at each visit. The ventral position of both the stigma and the majority of the anthers favor this (Fig. 7). That *Patagona gigas* is more than an occasional visitor to *E. atacamensis* subsp. *pasacana* is supported by other observations (Fries, 1903, cited in Porsch, 1939). Johow (1921, cited in Porsch, 1939) observed these hummingbirds also visiting the Chilean columnar cactus *Echinopsis litoralis* (Johow) H. Friedrich & G. D. Rowley (=*Trichocereus litoralis*). In Peru, *Patagona gigas* visits the shrubby *Weberbauerocereus weberbaueri* (Sahley, 1996). According to these observations, as well as our own, we suggest that *Patagona gigas* is a regular, rather than an occasional floral visitor to Andean columnar cacti, and a potential pollinator.

Our study provides the first demonstration of hawkmoth visitation for flowers of *E. atacamensis* subsp. *pasacana*. Hawkmoth abundance was low during our study and may be strongly influenced by night temperatures and the availability of other nectar sources. However, *Manduca diffissa* was collected several times in this region of Argentina (Moré et al., in press), with a proboscis length of about 52–69 mm (Moré, unpublished data). Because *E. atacamensis* subsp. *pasacana* flowers have an average internal length of

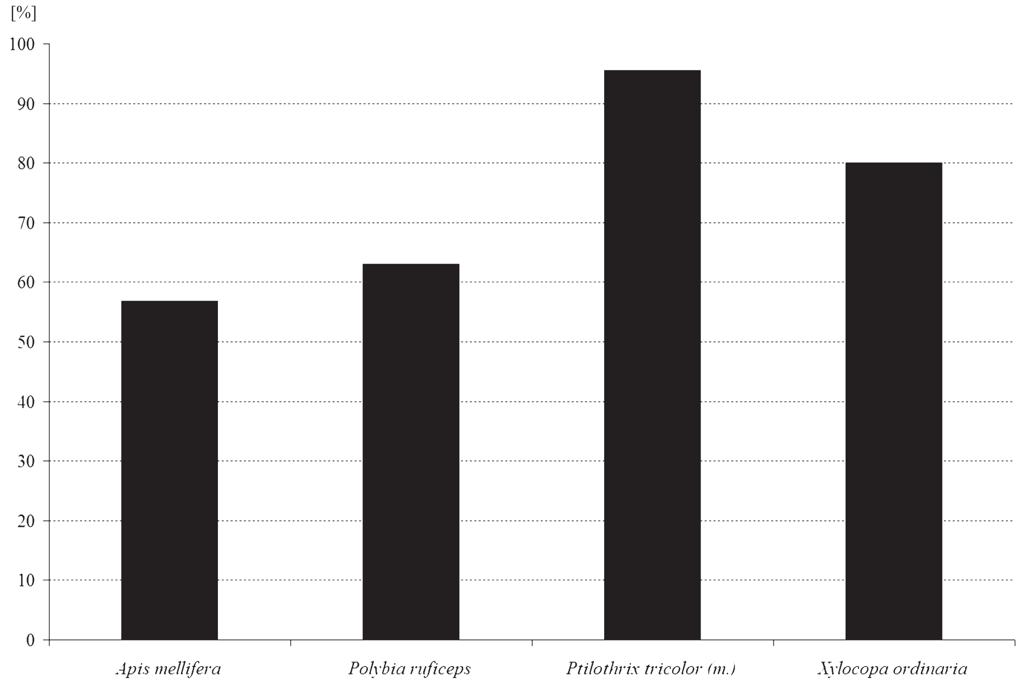

Figure 6. Percentage of stigma contacts by the most frequent flower visitors.

82.3 mm (de Viana et al., 2001), the hawkmoths have to crawl into the flowers to reach the nectary, as previously described for hawkmoths visiting flowers of *Datura* (Raguso et al., 2003). With this behavior the probability for efficient pollen transfer to the stigma is very high.

Higher precipitation, proximity of water and richer vegetation can easily explain the higher frequency and greater diversity of floral visitors at Site 1. However, higher abundance and diversity of floral visitors do not guarantee advantage in pollination success, which was greater at Site 2 (Badano and Schlumpberger, 2001). The activity of pollen-collecting *A. mellifera* may be one reason for the lower seed production that was observed at Site 1.

Despite the small sample size, our results support the suggestion that columnar cacti in extratropical regions tend to have a mixed pollination syndrome, which so far has only been demonstrated for one cactus species in South America, the shrubby *Weberbauerocereus weberbaueri* (Sahley, 1996). It is assumed that this mixed pollination syndrome helps cacti deal with between-year variation in pollinator presence (Sahley, 1996; Valiente-Banuet et al., 1997a, 1997b), in contrast to more stable conditions in the inner tropics, with often exclusively bat-pollinated species (Locatelli et al., 1997; Nassar et al., 1997). Our results further affirm that this mixed pollination syndrome, with similar floral characteristics, evolved at least twice: in North America in the tribe Pachycereeae, and in South America in the tribe Trichocereeae.

As the nocturnal anthesis and the nocturnal peak of nectar production (de Viana et al., 2001) indicate, nocturnal pollinators should play a role in the pollination of these cacti. However, during the study period in 2003 few visits by hawkmoths were observed, although nighttime temperatures were sufficient for hawkmoth activity. Identical light-trap setups in the same study period, but at lower altitudes, yielded high numbers of hawkmoths (data not presented here). Our observations indicate that the abundance of different pollinator species—especially birds and hawkmoths—may vary strongly in time, thus favoring an unspecialized pollination syndrome. Major factors for such variations may be the observed differences in temperature at night as well as strong variations in precipitation between years. In contrast to some other columnar cacti with this syndrome, like *Weberbauerocereus weberbaueri* or *Pachycereus pringlei* (Sahley, 1996; Fleming, 2002), *E. atacamensis* subsp. *pasacana* is self-incompatible and does not show strong intrapopulational variation in floral morphology (de Viana et al., 2001). Also, pollination by bats was not observed for *E. atacamensis* subsp. *pasacana*, although *Anoura geoffroyi* Gray (Chiroptera, Phyllostomidae) could possibly occur in these habitats (Fleming and Valiente-Banuet, 2002).

In the future, pollination efficiency of the different floral visitors of *E. atacamensis* subsp. *pasacana* should be analyzed. The importance

Figure 7. Cross-section of an *E. atacamensis* subsp. *pasacana* flower (arrow shows perforation at nectary caused by ants). Flower 129 mm long. **Figure 8.** *Patagona gigas* approaching a flower of *E. atacamensis* subsp. *pasacana*. **Figure 9.** *Patagona gigas* deeply entering a flower of *E. atacamensis* subsp. *pasacana* and feeding on nectar.

of nocturnal versus diurnal pollinators should be analyzed by pollinator-exclusion studies, and the possibility of year-to-year variations should be considered. Finally, the potential for pollination by nectar-feeding bats in these Andean habitats should be evaluated.

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