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Pollination biology of *Echinopsis leucantha* (Cactaceae): passerine birds and exotic bees as effective pollinators

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Abstract: Cactus flowers have traditionally been considered to be specialized to certain pollination guilds, but pollination studies reveal that most species are actually generalists. This suggests that floral traits are not always predictive of the animal visitors that pollinate cactus flowers. Here, we studied the pollination of *Echinopsis leucantha* (Gillies ex Salm-Dyck) Walp., an endemic cactus of Argentina, whose floral traits would suggest that it is pollinated by moths. The floral lifespan and flower availability throughout the reproductive period were evaluated. Field experiments were carried out to study the reproductive system and the identity and effectiveness of floral visitors. *Echinopsis leucantha* flowers had a nocturnal anthesis time that extended into the following morning. The species was self-incompatible. Floral visitors included moths, bees, and passerine birds. However, diurnal visitors were more effective as pollinators than nocturnal ones. The flowers of *E. leucantha* were phenotypically specialized (sphingophily); however, the pollination system was functionally and ecologically generalized. The results confirm that generalized pollination systems are widespread among species of the *Echinopsis* genus with nocturnal flowers, for which diurnal pollinators seem to have a key role in fruit and seed production. Our study constitutes the first record of passerine bird pollination in the Cactaceae for mainland South America.

Key words: Cactaceae, *Echinopsis*, floral syndrome, passerine, pollination.

Résumé : Les fleurs de cactus ont traditionnellement été considérées comme spécialisées envers certaines guildes de pollinisateurs, mais les études de pollinisation révèlent que la plupart des espèces sont en fait généralistes. Cela suggère que les traits floraux ne sont pas toujours prédicteurs des visiteurs animaux qui pollinisent les fleurs de cactus. Les auteurs ont étudié ici la pollinisation d'*Echinopsis leucantha* (Gillies ex Salm-Dyck) Walp., un cactus endémique de l'Argentine, dont les traits floraux pourraient suggérer qu'il est pollinisé par des papillons nocturnes. La durée de vie et la disponibilité des fleurs à travers toute la période de reproduction ont été évaluées. Des expériences sur le terrain ont été réalisées afin d'étudier le système reproducteur et l'identité et l'efficacité des visiteurs floraux. Les fleurs d'*E. leucantha* avaient une période d'anthèse nocturne qui s'étendait durant la matinée suivante. L'espèce était auto-incompatible. Les visiteurs floraux comprenaient les papillons nocturnes, les abeilles et les passereaux. Cependant, les visiteurs diurnes étaient des pollinisateurs plus efficaces que les visiteurs nocturnes. Les fleurs d'*E. leucantha* étaient spécialisées phénotypiquement (sphingophilie); cependant, le système pollinisateur était fonctionnellement et écologiquement généraliste. Les résultats confirment que les systèmes de pollinisation généralistes sont répandus chez les espèces du genre *Echinopsis* possédant des fleurs nocturnes, pour lesquelles les pollinisateurs diurnes semblent jouer un rôle clé dans la production de fruits et de graines. Leur étude est la première à rapporter une pollinisation par des passereaux chez des Cactaceae du continent sud-américain. [Traduit par la Rédaction]

Mots-clés : Cactaceae, *Echinopsis*, syndrome floral, passereau, pollinisation.

Introduction

Most angiosperms have been found to have generalist pollination systems, and specialization is now believed to be less common than once supposed (Waser et al. 1996; Ollerton et al. 2009). This can be true not only for species that are recognized as generalists but also for species whose floral traits suggest specialization to a particular pollinator (Aigner 2001; Ollerton et al. 2009; Gorostiague and Ortega-Baes 2016). This emerging pattern represents a challenge in the study of plant–pollinator interactions, because researchers often associate particular floral traits with a specific pollinator or a functional group of pollinators.

It is not unusual for observations that do not fit the theoretical expectations to be considered exceptions or

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novelties. However, there is evidence that the abundance and effectiveness of pollinators is highly temporally and spatially variable (Herrera 2005; Ollerton et al. 2007). One of the consequences of this variability could be a reduction in the selective pressure pollinators exert on floral traits (Herrera 2005; Herrera et al. 2006). If pollinators cease to be reliable, plant reproduction might start to depend on new opportunistic or unexpected pollinators (Feinsinger 1978; Aigner 2001). Changes in the species composition of effective pollinator groups do not necessarily imply changes in floral traits (Aigner 2001). Therefore, the realized pollination systems of a plant could be determined by the degree of phenotypic specialization (or generalization) shown by the plant (sensu Ollerton et al. 2007), as well as by the fluctuating environmental context of the plant's habitat (Aigner 2001; Ollerton et al. 2007).

The Cactaceae provide a good model to explore pollination systems because of their great floral diversity. Traditionally, cactus flowers are considered to be phenotypically specialized to certain pollinator types that include birds, bats, moths, and bees (Gibson and Nobel 1986; Pimienta-Barrios and del Castillo 2002). Nevertheless, most of the systems that have been closely studied are actually generalist, and documented cases of specialization are rare (Fleming et al. 2001; Ortega-Baes et al. 2011; Gorostiague and Ortega-Baes 2016). For example, pollination by birds has been recognized for several cactus species. The majority of these species present flowers that are phenotypically specialized to birds, with reddish corollas and tubular shapes. However, it has been demonstrated that these traits do not always represent functional specialization to bird pollination (i.e., they are not pollinated exclusively by birds). This suggests that, at least for this group of plants, floral traits are not always predictive of the pollinators that visit them. On the other hand, some cacti species that have been observed to be pollinated by birds do not have the phenotypic traits associated with this type of pollinators (Gorostiague and Ortega-Baes 2016; Martins et al. 2016).

The diverse genus *Echinopsis* includes globose to columnar cacti with widely variable phenotypical specialization in their flowers. Schlumpberger and Renner (2012) analyzed the phylogenetic relationships of the genus and suggested that pollination shifts (e.g., from bee flowers to hawk-moth flowers) are a common trait in the evolution of the genus. This idea is based on the assumption that the floral traits necessarily imply a pollination system that is specialized to birds, bees, or moths (Schlumpberger and Renner 2012). However, the assumption may not be accurate, because it does not consider the actual ensemble of pollinators that interact with different species of *Echinopsis*. Although there have only been a few studies to date, *Echinopsis* species with white flowers and nocturnal anthesis are assumed to be specialized to moth pollination. However, the species that

have been studied show floral cycles that extend into the following morning and have generalist pollination systems with both nocturnal (moth) and diurnal (bee and hummingbird) animals as effective pollinators (Schlumpberger and Badano 2005; Schlumpberger et al. 2009; Walter 2010; Ortega-Baes et al. 2011; Ossa and Medel 2011; Alonso-Pedano and Ortega-Baes 2012; Ortega-Baes and Gorostiague 2013). The role of these animals as pollinators seems to be variable among species. Nocturnal pollinators have a more important role in some species (Ortega-Baes et al. 2011), whereas others depend on diurnal pollinators (Schlumpberger and Badano 2005). Additionally, the two sets can be equally important or complementary (Walter 2010; Alonso-Pedano and Ortega-Baes 2012). These studies also suggest that the contribution to fruit and seed production by diurnal pollinators may be more important for species or populations in more arid environments (Schlumpberger et al. 2009; Walter 2010; Ossa and Medel 2011). The latter could be a consequence of the low nocturnal pollinator effectiveness at the distributional limits or more stressful sites, which could lead to the complementary pollination by diurnal visitors (Munguía-Rosas et al. 2009; Schlumpberger et al. 2009). Thus, the floral traits shown by this group of species within genus *Echinopsis* (i.e., phenotypical specialization to moths) do not necessarily correspond to their actual floral visitors. Such examples highlight the importance of documenting the role of floral visitors in plant reproduction rather than relying on predictions based on their phenotypical traits, especially for self-incompatible species that depend on floral visitors to produce fruits and seeds.

Here, we present the first record of passerine bird pollination for mainland South American cacti: the columnar cactus *Echinopsis leucantha* (Gillies ex Salm-Dyck) Walp. Although bird pollination has been recognized in many cacti species, it is mostly performed by hummingbirds (Trochillidae; Gorostiague and Ortega-Baes 2016). Only two cases of non-hummingbird pollination in cacti have been recognized: the pollination by doves (and other birds) of *Carnegiea gigantea* in North American deserts (Fleming et al. 2001; Drezner 2014), and the pollination by finches of *Opuntia* sp. in the Galápagos Islands (Grant and Grant 1981).

Echinopsis leucantha is a short columnar cactus endemic to the arid zones of Argentina. Its white nocturnal flowers present morphological traits associated with moth pollination, which suggest that moths could be their principal pollinators. This species was classified by Schlumpberger and Renner (2012) as pollinated by sphingids. Based on the available information about reproductive biology of other species of the genus prior to conducting the study, we hypothesized that: (*i*) fruit and seed production in *E. leucantha* depends on the service of its pollinators; (*ii*) this species has an extended floral cycle that allows diurnal visitors to effectively pollinate its

Fig. 1. *Echinopsis leucantha* individual (A) and a detail of its white flowers (B), which can be pollinated by the passerine bird *Phrygilus gayi* (C and D). [Colour online.]

flowers, and therefore it has a functionally generalized pollination system; and (*iii*) because this species is distributed in arid zones, diurnal pollinators (birds and (or) bees) have a more important role in fruit and seed production than nocturnal ones.

Materials and methods

Study species and site

Echinopsis leucantha is a short columnar cactus endemic to Argentina that reaches 1–1.5 m in height (Hunt 2006; Fig. 1A). Its flowers are hermaphroditic, white, and funnel-form, without odor (Fig. 1B), 198.17 ± 13.20 mm in length, and 113.62 ± 21.74 mm in diameter. Gynoecium length is 153.10 ± 13.30 mm, and the length of the largest stamen is 163.31 ± 14.99 mm. Each flower produces an average of 8.02 ± 9.85 μL of nectar (P. Gorostiague, unpublished data). Seeds are positively photoblastic and nondormant (Ortega-Baes et al. 2010*a*, 2010*b*).

The study was carried out in the El Obelisco (Salta province, NW Argentina; –26.0055 S, –65.7872 W). The site mean annual temperature is 16.4 °C, and the annual precipitation is 216 mm (Hijmans et al. 2005). This site corresponds to the High Monte ecoregion (Olson and Dinerstein 2002). The study was conducted during several reproductive periods (in 2011, 2012, 2013, and 2014), but the data presented here were recorded almost exclusively during November 2012, owing to low or null flower production in the other periods.

Floral lifespan

Twenty floral buds were tagged and covered with voile bags to prevent floral visitor activity. The phenological stage (floral bud, flower partially open, flower completely open, flower partially closed, and flower completely closed) was recorded every hour until senescence. Additionally, stigma receptivity was tested by hand cross-pollinating 12 flowers at night (2300 h) and 12 flowers at daytime (1000 h). These flowers were selected from a total of 19 individuals, with an average of 1.26 ± 0.45 (mean ± SD) flowers per individual.

To estimate the availability of flowers in the studied population, the total number of flowers produced was recorded for the reproductive periods from 2011 to 2014. Flower production was recorded from the appearance of the first flower until the closing of the last one on sixteen 10 m × 10 m randomly chosen quadrats every week.

Reproductive system

An experiment on the reproductive system of the species was performed during November 2012. It consisted of four treatments: (*i*) autonomous self-pollination (*n* = 21 flowers); (*ii*) manual self-pollination (*n* = 22); (*iii*) manual cross-pollination (*n* = 24); and (*iv*) natural (nonmanipulated) pollination (*n* = 24). Flowers in treatments *i*–*iii* were protected from floral visitors with voile bags. Flowers per treatment (*n* = 24) were randomly selected from a total of 96 floral buds from 69 individuals, with an average of

1.39 ± 0.49 (mean ± SD) buds per individual. Differences in sample sizes among treatments were caused by the loss of some buds following experimental manipulation. Because of the limited flower availability, it was not possible to test every treatment on each individual and use individuals as blocks. The response variables were fruit set and seed set. Differences between treatments were tested using a χ^2 test. Partitions of χ^2 tests were made to locate differences among the treatments (Agresti 2002). Statistical analyses were carried out using InfoStat software (Di Rienzo et al. 2013).

Floral visitors and their effectiveness

Floral visitors were recorded by focal observations of 20 flowers for 15 min every hour during three consecutive nights and the following days. Additionally, five flowers were videotaped for 15 min every hour from 2000 to 2400 h using an infrared filter on two consecutive nights. Floral visitors were only recorded for three days because the population did not produce more flowers. Bees were captured using hand nets, whereas birds were photographed and identified using a field guide (Narosky and Yzurieta 2010). To capture nocturnal moths, a UV-light trap was set in the study area from 1900 to 0100 h for 15 min of every hour during two consecutive nights. We also collected 40 stigmas from closed flowers of 40 randomly chosen individuals on two days (20 stigmas each day), which were transported to the laboratory and examined for moth scales. Floral visitor censuses were only carried out in the 2012 reproductive period. The population was also monitored during the 2011, 2013, and 2014 seasons, but in those years, the flower production was extremely low or nonexistent (see Results section).

To evaluate the effectiveness of diurnal vs. nocturnal floral visitors, we performed an experiment of three treatments: (*i*) natural pollination (nonmanipulated; *n* = 24 flowers); (*ii*) diurnal pollination (flowers excluded with voile bags before opening and taken off at dawn; *n* = 16); and (*iii*) nocturnal pollination (flowers excluded with voile bags during the day from dawn and until closing; *n* = 12). These flowers were selected from a total of 41 individuals, with an average of 1.29 ± 0.51 (mean ± SD) flowers per individual. We also performed an exclusion experiment for diurnal visitors with two treatments: flowers visited by bees and birds (*n* = 10 flowers) and flowers visited only by bees where birds were excluded using a 25 mm wire mesh that covered the whole plants (*n* = 14). Flowers used in this experiment were selected from a total of 20 individuals, with an average of 1.20 ± 0.41 (mean ± SD) flowers per individual. Flowers were excluded with voile bags before opening and taken off at dawn. For both experiments, the response variable was fruit set.

Results

Floral lifespan

The floral cycle began during the afternoon at 1800 h. All flowers were completely open at 2000 h and remained open until the following morning. By noon, flowers started to close, and all flowers were completely closed in the afternoon. The floral cycle of each flower lasted 22.7 ± 3.3 h (mean ± SD), and flowers lasted only one day. There were no significant differences for stigmatic receptivity (fruit set) between nocturnal (0.33) vs. diurnal (0.25) treatments (χ^2 = 0.2; *p* = 0.6534; df = 1).

Flower production was extremely low in 2011 (a total of only two flowers for the entire reproductive period) and 2013 (two flowers), and there were no flowers in 2014. During 2012, flowers were produced synchronously for three days. Total flower production in 2012 was 4.96 flowers/hectare (31 flowers), with an average of 1.11 flowers/individual.

Reproductive system

The reproductive system experiment showed significant differences among treatments (χ^2 = 19.96; *p* = 0.0002; df = 3). Automatic self-pollination and hand self-pollination treatments did not produce fruits. Fruit set for natural pollination (0.42) and manual cross-pollination (0.29) was not significantly different (χ^2 = 0.82; *p* = 0.3653; df = 1). However, seed set (mean ± SE) for hand cross-pollination (0.71 ± 0.12) was significantly higher (χ^2 = 1013.21; *p* < 0.0001; df = 1) than for natural pollination (0.51 ± 0.08).

Floral visitors and their effectiveness

During diurnal observations we recorded a total of 35 visits by bees (*Apis mellifera*, Apidae) and five visits by the gray-hooded sierra finch (*Phrygilus gayi*, Thraupidae; Figs. 1C and 1D). We did not record nocturnal visits by moths, nor did we capture moths on the UV-light trap. However, we found moth scales on 20.5% of the collected stigmas.

The effectiveness experiment showed significant differences among treatments (χ^2 = 8.89; *p* = 0.0117; df = 2). Nocturnal pollination did not result in fruit production. The fruit set value for diurnal pollination (0.25) did not differ from the natural pollination (0.42) treatment (χ^2 = 0.96; *p* = 0.3264; df = 1). The exclusion experiment for diurnal pollinators indicated that bees and birds were as effective as bees alone (χ^2 = 2.37; *p* = 0.1236; df = 1), with fruit sets of 0.6 and 0.29, respectively.

Discussion

Echinopsis leucantha flowered with nocturnal anthesis time, and flowers remained open into the following day. An extended floral cycle in species with nocturnal anthesis might be interpreted as a mechanism of reproductive insurance for pollination systems in which nocturnal visitors are less reliable pollinators. Such extended cycles ensure that flowers are available for nocturnal as well as for diurnal visitors. Diurnal pollinators can make a com-

plementary contribution to the fruit set of cacti species, or they can be more effective pollinators than nocturnal visitors (Fleming et al. 2001). This reproductive strategy places the pollination systems of cacti (and other desert plants) in a generalist category, especially for species of extra-tropical deserts (Fleming et al. 2001; Munguía-Rosas et al. 2009). Previously studied species of *Echinopsis* from extra-tropical South America also exhibited this strategy (Walter 2010; Ortega-Baes et al. 2011; Alonso-Pedano and Ortega-Baes 2012).

Our results indicated that *E. leucantha* is self-incompatible; i.e., it depends on pollen vectors to produce fruits and seeds. We did not register vegetative propagation for this particular species, so the recruitment seems to occur only through sexual reproduction. Self-incompatibility has proven to be a common trait among *Echinopsis* species, with *E. chiloensis* as the only recorded exception (Walter 2010; Ortega-Baes et al. 2011, Alonso-Pedano and Ortega-Baes 2012; Ortega-Baes and Gorostiague 2013). Our results showed that in the studied population, the fruit production of *E. leucantha* would be resource limited. It is likely that this limitation is associated with the arid climatic conditions of the study area (see below). On the other hand, the difference registered in seed set suggests that pollen also limits seed production. Low seed production because of scarce or ineffective pollinator visits is a widespread phenomenon among *Echinopsis* species (Ortega-Baes et al. 2011; Alonso-Pedano and Ortega-Baes 2012; Ortega-Baes and Gorostiague 2013).

We did not record (by direct observations, UV-light traps, or videotapes) moths or other nocturnal animals visiting the flowers of *E. leucantha*. However, some flowers had moth scales on their stigmas, suggesting that these animals are indeed floral visitors. The low proportion of stigmas with moth scales and the absence of moths in the UV-light traps suggest a low local abundance of this group of animals, as has been indicated for other pollination systems of cacti in north-western Argentina (Ortega-Baes and Gorostiague 2013). It is likely that the unpredictable flower resources are one of the causes of the low (or null) visitation rate by this group of animals and other potential pollinators. Flowering of *E. leucantha* occurs synchronously throughout a few days, and only in some years in the population studied. The only diurnal visitors were the exotic bee *Apis mellifera* and the grey hooded sierra finch *Phrygilus gayi*. During the study, bees were the most frequent visitors, and they entered the flowers for pollen. Finches posed on the flowers and fed on stamens and petals, touching the stamens and the stigma during their visit. Previous reports indicate that the diet of some species of the genus *Phrygilus* include fruits, nectar, and floral parts such as petals or stamens (McGehee and Eitniear 2007). Even when birds damage flowers during this process, passerine birds with this behavior can act as effective pollinators, providing a net benefit for the plant (Grant and Grant 1981). The present study reports the first record of passerine birds as pollinators of cacti in mainland South America. Only two other cases have been recorded in the cactus family: *Opuntia* sp. from the Galápagos Islands (pollinated by finches; Grant and Grant 1981), and *Carnegiea gigantea* from North America (pollinated by verdins, finches, and others; Drezner 2014).

According to our results, only diurnal visitors were effective pollinators of *E. leucantha* because no fruits were produced from the nocturnal pollination treatment. This supports our hypothesis that diurnal visitors are more important as pollinators in stressful environments. Other studies on *Echinopsis* indicated that both diurnal and nocturnal pollinators can contribute to total fruit set. Their contribution is complementary in some cases (e.g., *E. chiloensis* and *E. schickendantzii*; Walter 2010; Alonso-Pedano and Ortega-Baes 2012), but in other cases either nocturnal (e.g., *E. terscheckii*; Ortega-Baes et al. 2011) or diurnal (e.g., *E. atacamensis*; Schlumpberger and Badano 2005) floral visitors are more important. Therefore, all of the species in this group show phenotypical specialization to moth pollination; however, they have generalist pollination systems where the relative contribution of diurnal and nocturnal floral visitors is variable. Our study, as well as previous ones, highlights the need for comprehensive research that includes effectiveness experiments to describe plant–pollinator interactions and classify them as generalists or specialists (Gorostiague and Ortega-Baes 2016).

The conclusions about the pollination biology of *E. leucantha* presented in this manuscript are based on the study of one population during one reproductive period, and they should therefore be taken cautiously. Both the identity and the effectiveness of floral visitors might vary temporally and spatially. However, additional observations and experiments could not be carried out because the population did not produce flowers or production was very low during other study years (2010, 2011, 2013, and 2014). In this population, the reproduction of *E. leucantha* could depend on episodic flowerings such as the one that we observed. This process is most likely limited by the availability of resources such as water (a limitation that was also evidenced by the low fruit production). Generally, water input determines plant phenology in arid environments (Noy-Meir 1973), where reproduction can be pulsed (Ostfeld and Keesing 2000; Godínez-Alvarez et al. 2003). In this context, the resources offered by the flowers in this population would constitute pulsed resources that can be exploited (or not) by opportunistic floral visitors. The migrant gray hooded sierra finch could be one of the opportunistic pollinators that are not reliable for the plant, and the plant does not represent a constant and predictable floral resource for the birds, either. Thus, the temporal match or mismatch between the potential pollinators and floral resources

would be essential for establishing this plant–animal interaction.

Our findings support the idea that the specialization or generalization of pollination systems is not solely determined by the phenotypic traits of the flowers but also by the environment and its variability (the "set vs. setting" concept; Ollerton et al. 2007). The species studied here is considered to be specialized for moth pollination (Schlumpberger and Renner 2012), but our results show that it is actually generalist. Moreover, its most effective pollinators were diurnal visitors, contrary to what was expected (e.g., according to the most effective pollinator principle; Stebbins 1970). Other *Echinopsis* species with white nocturnal flowers also present generalist pollination systems, with extended floral cycles and a variable contribution by nocturnal and diurnal visitors. Based on the current evidence, we predict that, at least outside the tropics, all cacti species with nocturnal flowers could behave as generalists. However, at least for tribe Trichocereeae, the generalization of pollination systems seems to be independent of geographic location because tropical species show the same behavior (*Oreocereus celsianus*; Larrea-Alcázar and López 2011; *Weberbauerocereus weberbaueri*; Sahley 1996). Further studies on species of the tribe Trichocereeae and other linages (e.g., genera *Stetsonia* and *Cereus*) that inhabit the tropics and extra-tropics of the American Southern Hemisphere are necessary to test the ideas presented here. This will help to better understand the interactions among cacti with nocturnal flowers and their pollinators in this region of the Americas.

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