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POLLINATION ECOLOGY OF *AGAVE MACROACANTHA* (AGAVACEAE) IN A MEXICAN TROPICAL DESERT. II. THE ROLE OF POLLINATORS[1]

SANTIAGO ARIZAGA,[2] EXEQUIEL EZCURRA,[3] EDWARD PETERS,[2]
FERNANDO RAMÍREZ DE ARELLANO,[2] AND ERNESTO VEGA[2]

[2]Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 27–3 (Xangari), 58190–Morelia, Michoacán, Mexico; and
[3]Biodiversity Research Center of the Californias, San Diego Natural History Museum, P.O. Box 1390, San Diego, California 92112 USA

We did a series of observational studies and manipulative experiments on the guild of nocturnal visitors of *Agave macroacantha*, including (1) a description of the hourly patterns of visits by moths and bats, (2) an evaluation of the relative contribution of bats and moths to flowering success, and (3) an evaluation of the pollination efficiency of the different bat species. Scapes exposed to moths but excluded to bats yielded ~50% fewer fruits than those exposed to both pollinator groups. Flowers exposed to the bat species *Leptonycteris curasoae* showed similar fruiting success to those exposed to *Choeronycteris mexicana* and to those exposed to the whole nocturnal visitor guild. However, the fruits originated from flowers pollinated by *Leptonycteris curasoae* yielded significantly more seed than those exposed to *Choeronycteris mexicana* or to the whole pollinator guild. It is concluded that *Agave macroacantha* is extremely dependent on nocturnal pollinators for its reproductive success and that bats are especially important for successful pollination. Some of these pollinators are migratory and have been reported to be steadily declining. A continuing decline in the populations of pollinators may impede the successful sexual reproduction of the plant host and may put the long-term survival of this agave species under risk.

Key words: *Agave macroacantha*; deserts; fruit set; Mexico; moths; nectar-feeding bats; pollination biology; pollinator effectiveness; rosette plants.

Agave macroacantha is a semelparous plant with succulent leaves arranged in basal rosettes. It is endemic to the Tehuacán-Cuicatlán tropical desert, in south-central Mexico. The reproductive individuals develop between May and June a paniculate inflorescence, or scape, that takes approximately a month to mature (Gentry, 1982; Arizaga and Ezcurra, 1995; Arizaga et al., 2000). The flowers are hermaphroditic, protandric, and alogamous. Nectar production, anthesis, and stigmal receptivity develop basically during the night, a flowering syndrome that has been associated with pollination by nectarivorous bats (Faegri and van der Pijl, 1971; Howell, 1974, 1979; Schaffer and Schaffer, 1977). In agreement with the nocturnal timing of floral receptivity, nighttime visitors are almost exclusively responsible for pollination (Arizaga et al., 2000).

Several authors (e.g., Howell, 1974, 1979; Schaffer and Schaffer, 1977; Howell and Roth, 1981; Freeman and Reid, 1985; Fleming, Núñez, and Sternberg, 1993) have pointed out that paniculate agaves (generally belonging to the subgenus *Agave*; Gentry, 1982) are pollinated chiefly by bats, while spiculate agaves (mostly members of the subgenus *Littaea*) are pollinated generally by insects. Few studies, however, have demonstrated the association between bats and paniculate agaves (Howell, 1974; Howell and Roth, 1981), and none has evaluated the effect experimentally. Moreover, there is a large literature documenting the role of bats as pollinators of diverse plant taxa (for a revision see Butanda-Cervera, Vázquez-Yanes, and Trejo, 1978) , but in all of them the evidence is mostly observational, either documenting pollen or flower remains in bats collected in the field or inferring chyropterophilia from the flowering syndrome and the floral morphology. Three bat species have been reported as pollinators of agaves: *Leptonycteris curasoae* Miller, *L. nivalis* (Saussure), and *Choeronycteris mexicana* Tschudi (Álvarez and González Quintero, 1970; Easterla, 1972; Howell, 1979; Howell and Hart; 1980; Howell and Roth, 1981). In contrast, the role of nocturnal Lepidoptera (moths) as pollinators of Agavaceae has been poorly documented, with the exception of the mutualism between the moth *Tegeticula* spp. and *Yucca* plants (Rau, 1945; Aker and Udovic, 1981; Craig et al., 1993; Villavicencio and Pérez-Escandón, 1995). A number of moth species belonging to the families Noctuidae and Sphingidae, as well as a number of nocturnal Microlepidoptera, have been observed visiting the inflorescences of some Agavaceae (Howell and Roth, 1981; Freeman and Reid, 1985; Eguiarte and Búrquez, 1987, Arizaga et al., 2000), a fact that may lead one to hypothesize that they may also play a role in the pollination of flowers in the scapes (Arizaga et al., 2000).

Understanding the reproductive biology of agaves and its links with the guild of pollinators is of great importance, as the destruction of the natural habitats of these

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plants is putting under increasing risk the livelihood of a number of animal species whose survival depends on agaves through a complex set of biotic interactions including the consumption of agave nectar (Gentry, 1972; Howell and Roth, 1981; Waring and Smith, 1987; Nabhan, 1994). In this paper we present a series of experimental studies with *Agave macroacantha* in the Tehuacán-Cuicatlán desert, done with two main objectives: (1) to understand the differential role of bats and moths in the pollination of *A. macroacantha*, and (2) to evaluate which of the bat species visiting the plant is the most effective pollinator. To our knowledge, this is the first study that experimentally evaluates the reproductive success of an agave plant in relation to its pollinator guild by manipulating the different bat species and by differentially separating the effect of the nocturnal pollinators.

MATERIALS AND METHODS

Study area—The experiments were done between April and October 1996 at the field laboratory of UNAM's Institute of Ecology, located in Zapotitlán Salinas (18°20′ N, 97°28′ W; for a detailed description of the study area see Zavala-Hurtado, 1982; Arizaga et al., 2000).

Hourly patterns of visits by bats to agave patches of different sizes—In April 1996, we collected 50 individual rosettes of *A. macroacantha* that were starting to produce scapes and transplanted them to an enclosure, which was protected from large herbivores but open to the arrival of pollinators. In July, once the scapes had developed in all rosettes, we transplanted them to the field under natural conditions, in a protected plot of land where we could follow their floral development. In order to simulate the clustered distribution of *A. macroacantha* under natural conditions in the field, we planted the flowering rosettes in three clusters or patches. Plants within each cluster were ~1 m apart from their nearest neighbors, and clusters were separated by 50 m. The patches had 21, 10, and 19 scapes, respectively. The plants in first two patches were in the stage of flowering initiation in their lower umbels, while the plants in the last patch had initiated flowering ~1 mo before the transplant and were in the stage of capsule formation. Thus, we formed (1) a large patch (N = 21 scapes) with receptive flowers, (2) a small patch (N = 10 scapes) with receptive flowers, and (3) a large patch (N = 19 scapes) with nonreceptive flowers. In each patch we counted (1) the number of flowers developed in each scape and (2) the number of bats visiting the patch during 4 d, every hour from 2100 to 0600 (local meridian time), during a 5-min interval of observation. In October, once capsule formation ended in all plants, we counted the number of fruits (capsules) in each scape and the number of viable seeds per capsule in randomly selected capsules.

Hourly patterns of visits by moths—In the large (N = 21 scapes) patch described in the previous paragraph, we also counted during 4 d the number of moths (Lepidoptera) visiting the patch in 5-min observation intervals spaced every hour from 2130 to 0630 (moth counting was started on 18 June 1996, the next day after bat counting ended, when the scapes still showed a high number of receptive flowers). We also recorded the flowering stage of the flowers that were reached by moths, classifying the stages into three categories (pistillate, staminate, and other). Once the 5-min observation period ended, we initiated a second observation period in which we followed individual moths, counting the number of times they changed from one flower to another and registering whether the flower belonged to the same individual scape or to a different one. Two moths (Lepidoptera: Noctuidae) were followed, for 5-min each, in each hourly observation period. Thus, we could estimate the proportion of visits that are preceded by visits to different flowering stalks, and we were able to evaluate how this proportion changes during the night.

Evaluation of the contribution of bats and moths to flowering success—Nine flowering rosettes were transplanted to a 4 × 4 m plot. To decrease the probability of wind-pollination, a polyethylene plastic sheet was installed surrounding the plot at a height of 1–3 m (pollinators, however, could fly into the plot from above or below the plastic). Three randomly chosen scapes were enclosed inside a gauze-covered wire-mesh structure that impeded the access of both bats and moths. Other three scapes were surrounded by a wire-mesh structure with no gauze covering, to impede the access of bats but allow that of moths (mesh size was ~2.5 cm). Finally, the remaining three scapes were left uncovered and hence open to all pollinators. In each scape we counted the number of flowers produced, the number of capsules at the end of flower development, and the number of viable seeds per capsule in nine randomly selected capsules (three capsules per individual).

Evaluation of the pollination efficiency of the bat species—Five individuals of *Choeronycteris mexicana* and eight of *Leptonycteris curasoae* were collected with mist nets and kept in captivity under a diet of synthetic nectar, water, and fresh cactus fruits [we used fruits of *Stenocereus griseus* (Haworth) Buxbaum and *Stenocereus stellatus* (Pfeiffer) Riccobono]. Eight flowering rosettes were collected in the field when ~30% of the umbellate clusters in the scape had already opened their flowers and had thus been exposed to the complete set of pollinators under natural conditions. The plants were transplanted into a 4 × 4 m cage, covered with a plastic mesh that impeded the access of both bats and insects. As the flowering ''branches'' (i.e., the umbellate clusters of flowers at the end of long lateral peduncles) became receptive, they were assigned in alternating order to one of the two bat species. All odd-numbered umbels were exposed every two nights to two individuals of *Choeronycteris,* randomly selected from the captive group, while the even-numbered umbels were exposed every other night to two individuals of *Leptonycteris.* On the nights that a *Choeronycteris* was released into the cage, all even-numbered umbels were covered to avoid pollination, and similarly, all odd-numbered umbels were covered during the nights that *Leptonycteris* was released. The lower umbels were kept open during the entire experiment. The pair of bats was recaptured the next morning. The experiment was continued for 14 nights, each bat species having access to the cage during seven nights. Each evening before releasing the bats in the cage we counted and marked the receptive flowers that were exposed to the bat pollinators during the night. At the end of the experiment, we counted in each umbel the number of capsules produced at the end of flower development and the number of viable seeds per capsule in nine randomly selected capsules (three capsules per individual). Additionally, while the experiment was performed, we also measured the time employed by each bat species foraging on individual flowers. For this purpose, we installed a red light source on the cage, and observed the bats during three 1-h periods for 1 d: from 2200 to 2300, from 0200 to 0300, and from 0500 to 0600. During each observation period, we measured with a chronometer the time elapsed between the first contact and the departure of the bats from each flower. These time values were recorded for all the bat-flower contacts detected during the observation period.

Statistical analyses—All the statistical analyses we used are described in more detail in Arizaga et al. (2000). The relationship between frequency variables and their statistical predictors was analyzed by means of Poisson regression (Crawley, 1993; Everitt, 1994; Krause and Molson, 1997). Proportions were analyzed by means of logistic models (Crawley, 1993). In both cases, we rescaled the data when correction for overdispersion was necessary (Crawley, 1993). We used standard ANOVAs to analyze continuous variables with normal errors. In all cases, the analyses were made with the GLIM (Generalized Linear Interactive Modeling) statistical package, version 3.77 (McCullagh and Nelder, 1983; NAG, 1986). When the response variables were obtained from repeated measurements, we followed the procedure suggested by

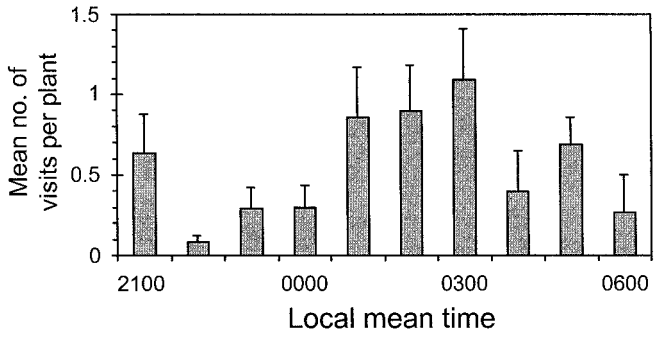

Fig. 1. Hourly pattern of visits by bats to agave scapes in the field. The vertical lines indicate 1 SE.

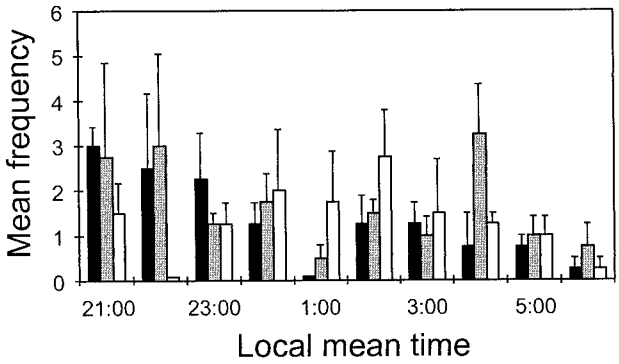

Fig. 2. Hourly pattern of mean number of visits by moths to *Agave macroacantha* flowers in the field. The vertical lines indicate 1 SE. Black bars = developing flowers; hatched bars = staminate flowers; white bars = pistillate flowers.

von Ende (1993). To facilitate comparisons, time measurements were converted to local mean time (i.e., the time of the local meridian).

RESULTS

Hourly patterns of visits by bats to agave patches of different sizes—The patch with fruiting scapes and hence showing nonreceptive flowers (patch 3) did not receive the visit of any pollinator during the span of the observation period. Because its statistical behavior was so obviously different from the other two patches that had receptive flowers, it was removed from subsequent analyses. The small patch (patch 2) received significantly fewer visitors than the larger patch ($\chi^2 = 19.6$; df = 1; $P < 0.0001$). Significant variation was also found between days nested within patches ($\chi^2 = 44.0$; df = 6; $P < 0.0001$) and between hours nested within days ($\chi^2 = 957.2$; df = 72; $P < 0.0001$). However, when the data were standardized to number of visits per plant, the difference between both patches became nonsignificant ($t = 0.53$; df = 4; $P = 0.62$); the mean number of nocturnal visits per plant was 5.82 (SE = 0.78) in the large patch and 5.18 (SE = 0.93) in the small patch. In spite of the significant differences between nights, most (96%) of the observed variation was attributable to the effect of hourly changes in pollinator activity. A significant ($\chi^2 = 281.9$; df = 18; $P < 0.0001$) hourly pattern was observed for both patches: Visits were more frequent in the early night, and decreased between 2200 and midnight. After midnight, the activity of pollinators increased again and decreased gradually after 0300 (Fig. 1). In harmony with the previous results that show a similar intensity of pollinator visits in all plants, the mean proportion of fruits set in each scape did not differ significantly between the three patches ($\chi^2 = 2.0$; df = 2; $P = 0.37$). The plants in the large patch, in the small patch, and those that had been exposed to pollination before the experiment showed, on average, ~11% of their flowers becoming capsules (SE = 3%).

Hourly patterns of visits by moths—No significant differences were found in the total number of moths visiting flowers in different phenological phases ($\chi^2 = 2.2$; df = 2; $P = 0.33$), but significant variations were found between days ($\chi^2 = 30.7$; df = 3; $P < 0.0001$) and between hours nested within days ($\chi^2 = 79.0$; df = 36; $P < 0.0001$). The daily variation observed was mostly due to the fact that during the first night (18 June 1996) significantly more visits were received than during the other three nights in which we counted moth arrivals. In all days a significant ($\chi^2 = 30.2$; df = 9; $P = 0.0004$) hourly trend was found. The total number of visits clearly showed two peaks: one at 2130 and the second one between 0230 and 0430 (Fig. 2). When this nocturnal pattern was tested for each phenological phase, a significant interaction between the phenological state and the hour of arrival of pollinators was found ($\chi^2 = 43.1$; df = 18; $P = 0.0008$). While moths visiting flowers that were neither staminate nor pistillate peaked after midnight at ~0230, the moths visiting pistillate flowers peaked later, at ~0430.

The proportion of flower-to-flower trips that were made within the same scape (56%) was significantly higher than that of flower-to-flower trips between different scapes (44%; $\chi^2 = 4.34$; df = 1; $P = 0.04$; we registered a total of 236 trips during the four-night observation period, 132 were within-scape and 104 were between-scape visits). The duration of visits of the individual moths was very constant. The number of flower-to-flower visits per moth did not vary significantly with the day or the hour. Additionally, the proportion of within-scape to between-scape visits was also quite constant and did not vary significantly during the observation period.

Evaluation of the contribution of bats and moths to reproductive success—There was a mean of 195.3 (SE = 23.8) flowering buds per scape and the observed variation in their numbers was independent from the treatments ($\chi^2 = 2.0$; df = 2; $P = 0.37$). The number of fruits decreased significantly ($\chi^2 = 9.4$; df = 2; $P = 0.009$) with the intensity of pollinator exclusion (Fig. 3). In contrast, it was found that some of the plants in the two exclusion treatments produced bulbils in the scape, while none of the control plants produced bulbils. Although a large overdispersion was found in the number of bulbils produced, after correcting for this effect and pooling the two treatments together the differences between the treatments and the control were found to be significant ($\chi^2 = 5.0$; df = 1; $P = 0.03$). In short, pollination exclusion leads to a lower production of fruits, but also triggers the production of bulbils.

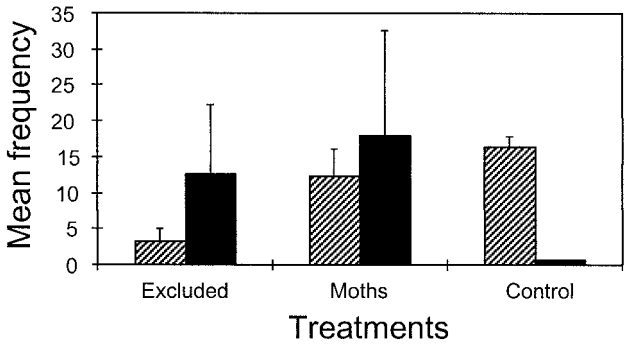

Fig. 3. Mean number of fruits (hatched bars) and bulbils (black bars) produced in scapes subject to three treatments. Excluded = scapes with impeded access to both bats and moths; moths = scapes with impeded access to bats, but with open access to moths; control = uncovered scapes. The vertical lines indicate 1 SE.

Additionally, the exclusion of pollinators also decreased significantly the number of seeds per fruit (χ^2 = 52.6; df = 2; $P < 0.0001$; Fig. 4), although the effect of individual rosettes nested within treatments was also found to be highly significant (χ^2 = 99.9; df = 6; $P <$ 0.0001). That is, a high proportion of the observed variation is unrelated to the experimental treatment and attributable to independent features of the individual plants. The joint effect of pollinator exclusion on both number of fruits and number of seed per fruit has a multiplicative effect on the overall fecundity of the individual rosettes. While the control plants produced, on average, 2064 fertile seeds per scape, the moth-pollinated (bat-excluded) rosettes produced 772 seeds, and the individuals under complete exclusion of pollinators produced 153 seeds, that is, only 7% of the fecundity observed in the control plants.

Evaluation of the pollination efficiency of the bat species—The pollination efficiencies of *Choeronycteris mexicana* and *Leptonycteris curasoae* were not significantly different from the pollination-efficiency values observed under field conditions for the same plants (χ^2 = 1.3; df = 2; P = 0.52). In all three categories the mean fruit set was ~8.3% (SE = 0.9; fruit set was calculated as the percentage of fruit produced with respect to the

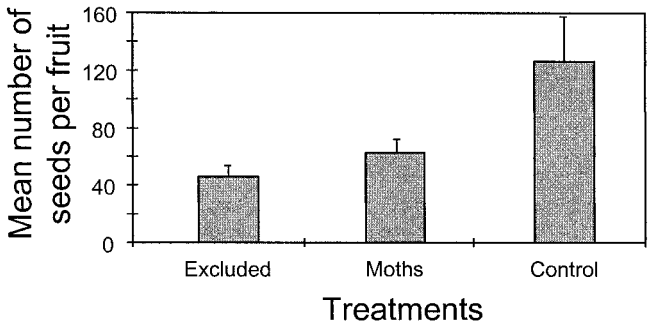

Fig. 4. Seed set (mean number of seeds per fruit) produced in nine randomly selected fruits from scapes subject to three treatments. Excluded = scapes with impeded access to both bats and moths; moths = scapes with impeded access to bats, but with open access to moths; control = uncovered scapes. The vertical lines indicate 1 SE.

Fig. 5. Adult individual of *Leptonycteris curasoae* feeding on a lateral umbellate cluster of flowers of *Agave macroacantha* inside the experimental cage.

number of flower buds initially available for each pollination treatment). There were, however, highly significant differences between individuals (χ^2 = 37.6; df = 7; $P <$ 0.0001); that is, some individuals produced a significantly higher fruit set than others in all branches independently of the treatment to which the branch had been exposed.

When the seed set per fruit was analyzed, it was found that those fruits that derived from flowers that had been exposed to *Leptonycteris* (Fig. 5) yielded significantly more seed than the fruits derived from control branches or from flowers that had been exposed to *Choeronycteris* (χ^2 = 8.2; df = 2; P = 0.016; Fig. 6). Highly significant differences were also found between individuals (χ^2 = 142.1; df = 7; $P < 0.0001$), but not between fruits nested within individuals (χ^2 = 19.1; df = 16; P = 0.26), nor for the interaction between treatments and individuals (χ^2 = 18.7; df = 14; P = 0.18). In short, *Leptonycteris*-pollinated flowers yielded more seed per fruit, but the strongest differences in fruit set were unrelated to the

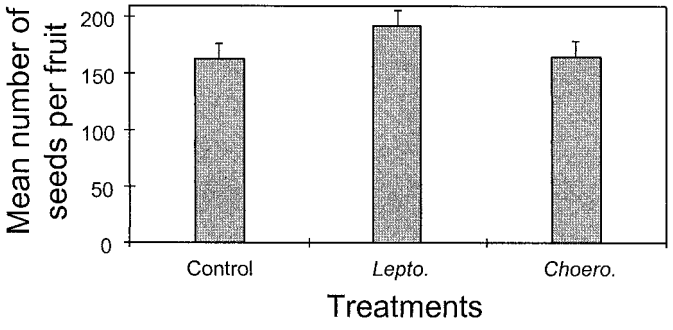

Fig. 6. Seed set (mean number of seeds per fruit) produced in nine randomly selected fruits from scape branches subjected to three treatments. Control = branches with open access to all pollinators in the field; *Lepto.* = branches with access open only to *Leptonycteris curasoae*; *Choero.* = branches with access open only to *Choeronycteris mexicana*. The vertical lines indicate 1 SE.

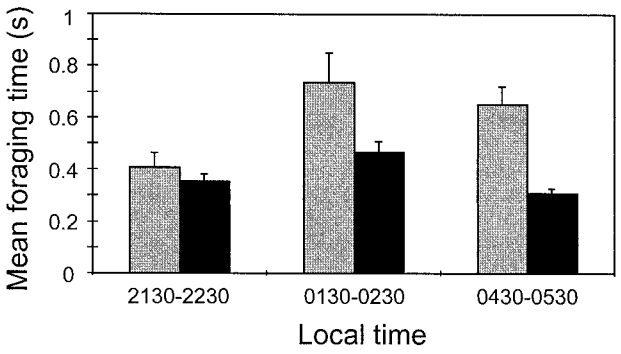

Fig. 7. Mean time employed by bats in collecting nectar from a single flower (foraging time) at different time periods during one night for the two bat species. Hatched bars = *Choeronycteris mexicana*; black bars = *Leptonycteris curasoae.* The vertical lines indicate 1 SE.

pollinator species and attributable to independent features of the individual plants.

Foraging times—The visiting time employed in each individual flower was significantly shorter for *Leptonycteris* than for *Choeronycteris* ($F = 23.7$; df = 1, 138; $P < 0.0001$; Fig. 7). Both species showed significant variation in their foraging times ($F = 3.4$; df = 2, 138; $P = 0.04$), and a similar pattern during the night they were studied. Foraging times were shortest at 2200–2300, increased to a maximum between 0200 and 0300, and decreased again before dawn (0500–0600). There was not a significant interaction term between the bat species and the hour during which the observations were made. In addition to the observed lengthier stays of *Choeronycteris* in each individual, it was also noted (outside our experimental observation periods) that *Choeronycteris* sometimes rested for a minute or more on a flowering branch, while the quicker and more active *Leptonycteris* was never observed perching or resting on the scape branches.

DISCUSSION

In our study, the bat guild proved to be the most efficient source of pollination of the allogamous *A. macroacantha,* more than doubling the seed set obtained in scapes that were visited only by moths. These results support the hypothesis put forth by different authors that paniculate agaves are pollinated chiefly by bats (Howell, 1974, 1979; Schaffer and Schaffer, 1977; Howell and Roth, 1981). Numerous authors (e.g., Alcorn, McGregor, and Olin, 1962; Álvarez and González Quintero, 1970; Easterla, 1972; Howell and Hodgkin, 1976; Howell, 1979; Howell and Hart, 1980; Fleming, Núñez, and Sternberg, 1993; for a revision see Arita and Martínez del Río, 1990) have suggested that the morphological, biochemical, and phenological characteristics of the paniculate agaves make them highly dependent on bats for their pollination. These bats belong chiefly to the genus *Leptonycteris,* a taxon that presents a set of fine morphological, physiological, and behavioral adaptations that allows feeding from nocturnal flowers (Arita and Martínez del Río, 1990).

Of the two bat species (*Leptonycteris curasoae* and *Choeronycteris mexicana*) we found visiting the flowers of *A. macroacantha, Leptonycteris* proved to be the most efficient pollinator, yielding almost 20% more seeds per fruit than *Choeronycteris. Leptonycteris curasoae* is a swift flyer and often perches briefly on the lateral branches of the scape to sip nectar from the internal flowers. This characteristic pattern has also been described for *L. nivalis* (Barbour and Davis, 1969; Faegri and van der Pijl, 1971), which is also an agile flyer capable of rapid maneuvers and with a quick flight (Hayward and Davis, 1964). In contrast, *C. mexicana* prefers flying in open spaces (Barbour and Davis, 1969) and was never observed perching on the flowering branches. The fact that bats did not visit patches with fruiting scapes strongly suggests that these two species of pollinator follow olfactory queues during their flights. In agreement with this hypothesis, Howell (1974) reported that the echolocation system in nectarivorous bats is poorly developed and that in contrast their senses of sight and smell are very acute (Arita and Martínez del Río, 1990).

Moths preferentially visited the staminate flowers, which are the ones that produce more nectar. Their nectar-feeding pattern consists in setting down on the outside of the flower, crawling on the tepals, and introducing the proboscis inside the corolla down into the nectaries. Possibly because of their smaller size and lower metabolism, they rest longer on each flower and usually move on to feed from flowers in the same scape. For this reason, moths were less efficient agents of cross-pollination than bats.

In conclusion, *A. macroacantha* is extremely dependent on nocturnal pollinators, especially on bats, for its reproductive success. Our data show that *Leptonycteris curasoae* is the most efficient pollinator of *A. macroacantha,* while *Choeronycteris mexicana* is second in importance. In a similar experimental study with giant columnar cacti as host plants, Alcorn, McGregor, and Olin (1961) have shown *Leptonycteris nivalis* to be the most effective pollinator of *Carnegiea gigantea* and *Lemaireocereus thurberi.* Although the moths that visit the flowers seem to be basically resident species, *Leptonycteris* and *Choeronycteris* bats are migratory (Cockrum, 1991) and have been reported to be steadily declining for a number of reasons, but principally through habitat deterioration (Barbour and Davis, 1969; Easterla, 1972; Howell and Roth, 1981; Tuttle, 1995). The three main species of nectarivorous bats in North America (*Leptonycteris curasoae, L. nivalis,* and *Choeronycteris mexicana*) migrate in winter from Southwestern United States into the Mexican plateau (Barbour and Davis, 1969; Arita and Wilson, 1987; Cockrum, 1991). They consume mostly nectar and pollen of agaves and cacti and also occasionally the sugary pulp of cactus fruits (McGregor, Alcorn, and Olin, 1962; Alcorn, McGregor, and Olin, 1962; Alvarez and González Quintero, 1970; Howell, 1979; Howell and Roth, 1981; Arita and Wilson, 1987; Cockrum, 1991; Fleming, Núñez, and Sternberg, 1993; Valiente-Banuet et al., 1996; a revision on chyropterophilic pollination is given in Butanda-Cervera, Vázquez-Yanes, and Trejo, 1978). During their migrations, they tend to follow ''nectar corridors'' along the Mexican highlands, seeking vegetation types where they may find a relatively dependable supply of flowers (Gardner, 1977). This complex migratory pattern has implications from a conservationist point

of view, as the disturbance of plant communities along the migration route may have a strong impact on the capacity of the bat populations to find their sustenance (Fleming, Núñez, and Sternberg, 1993).

Recent investigations have shown that the populations of *Leptonycteris* are decreasing at an accelerated rate (Barbour and Davis, 1969; Easterla, 1972; Howell and Roth, 1981; Arita and Wilson, 1987; Eguiarte and Búrquez, 1988). The U.S. Fish and Wildlife Service has classified the three species as endangered in the United States (Arita and Wilson, 1987). Ceballos and Navarro (1991) have described the same three species as threatened in Mexico. Habitat deterioration from cattle husbandry, agricultural developments, and logging, together with the direct killing of bats in their caves, are believed to be the main causes of bat decline in North America (Arita and Wilson, 1987; Ceballos and Navarro, 1991). The ecological role of bats enhances the viability of the agave populations not only at a demographic level, by increasing the seed set, but also at a genetic level, by increasing cross-fertilization between different agave individuals. In the Tehuacán Valley there are at least eight other wild species of paniculate agaves (of which the most important are *A. karwinskii*, *A. marmorata*, *A. potatorum* and *A. salmiana*). There are also some 30 species of columnar cacti (Dávila et al., 1993) that are possibly as dependent on bat pollination as *A. macroacantha*. A continuing decline in the populations of these pollinators may hinder the success of sexual reproduction in *Agave macroacantha* (and possibly of many other cacti and agaves) and may put the long-term survival of these important succulent plants at risk.

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