

POLLINATOR EFFECTIVENESS, POLLINATOR IMPORTANCE,
AND POLLEN DISPERSAL IN STAR CACTUS
(*ASTROPHYTUM ASTERIAS*)

THESIS

Presented to the Graduate Council of
Texas State University-San Marcos
In Partial Fulfillment
of the Requirements

for the Degree

Master of SCIENCE

by

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San Marcos, Texas
December 2007

ACKNOWLEDGEMENTS

I am grateful to my fellow graduate students at Texas State University-San Marcos who provided much needed emotional support and advice on how to navigate the sometimes tumultuous waters of graduate school and field research.

I would also like to acknowledge the members of the star cactus recovery team, Dr. Paula Williamson, Jackie Poole, Gena Janssen, Lisa Williams, Anna Strong, Sandy Birnbaum, and Adam Ferguson. I gained many valuable insights about plant conservation by working with these individuals in the field.

I am also indebted to Johnny Jisha, Cynthia Wendt, Anna Strong, and my brother Michael Blair for their generous sacrifices of time and energy to assist me with field work in south Texas.

Dr.'s Jim Ott and Chris Nice cannot be thanked enough for their advice and encouragement at every stage of this project and for the investments they've each made in my education and professional development over the last three years.

I am particularly grateful to Dr. Paula Williamson for her advice and support of my research and for helping me to grow and develop as a professional biologist.

And finally, I must thank my wife Brandi for her endless patience and support (emotional as well as financial), and my son Sean for helping me keep everything in perspective.

This manuscript was submitted on November 1, 2007.

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ABSTRACT

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Star cactus (*Astrophytum asterias*) is a federally endangered plant and from known records is restricted to a single south Texas county and a small number of sites in northeastern Mexico. Star cactus is an obligate outcrosser that does not reproduce vegetatively, so all reproduction is the result of inter-plant pollen transfer by insects. By measuring seed set resulting from single pollinator visits, I evaluated the pollinator effectiveness (mean seed set/visit) and pollinator importance (effectiveness * visitation frequency) of insect species visiting flowers of star cactus. Results indicate that the most common visitor, *Macrotera lobata*, is a relatively ineffective pollinator, while the less common *Diadasia rinconis* is the most effective and important pollinator of star cactus. Two behavioral variables (visit duration, whether or not visitors landed on the stigma) were assessed as possible predictors of fruit set. While visit duration was not predictive of fruit set, there was a positive correlation between fruit set and whether a

visitor landed on the stigma when entering the flower. In an additional study, fluorescent dye was used as a pollen analogue to track the distribution of pollen dispersal within a 1.9 hectare patch of star cactus. Dispersal distances between source and recipient plants were used to calculate estimates of genetic neighborhood size and area using Wright's neighborhood model. These neighborhood estimates (neighborhood size = 41.8 individuals, neighborhood area = 0.094 hectares) indicate the potential for population subdivision within the larger patch due to restricted pollen dispersal. The results of these studies will be used by conservation officials to inform management decisions.

I. INTRODUCTION

In the last decade, it has become clear that effective management of populations of rare plants must include understanding the community-level processes that affect these populations (Sipes and Tepedino, 1995; Corbet, 1997; Timmerman-Erskine and Boyd, 1999; Wall et al., 2003). The interactions between plants and their pollinators are of particular importance as many endangered plants are dependent on pollinators for reproduction and maintenance of viable populations (Nabhan and Flemming, 1993; Kearns and Inouye, 1997; Kearns et al., 1998; Spira, 2001; Wall et al., 2003). Pollination studies are especially important for rare plant species that are self-incompatible or that do not reproduce asexually (Bond, 1994). Understanding which flower visitors are the most effective and important pollinators of these plants is crucial to their recovery. Management decisions, such as the designation of critical habitat or the use of pesticides on nearby lands may need to take into account the needs of pollinators in order to ensure long-term survival of populations (Sipes and Tepedino, 1995; Havens, 1999).

Star cactus, *Astrophytum asterias* (Zuccarini) Lemaire, is a rare species, listed as federally endangered in 1993 and listed as endangered by the State of Texas in 1997 (USFWS, 2003). *Astrophytum asterias* is also included in Appendix I of CITES (Convention on International Trade of Endangered Species). While surveys are ongoing, star cactus is currently known to occur only on 14 properties in Starr County, Texas, and at 9 small sites in the neighboring Mexican states of Tamaulipas and Nuevo Leon

(Martinez-Avalos et al., 2004). Historically, *A. asterias* occurred over a larger portion of southern Texas and northern Mexico, but habitat destruction and modification along with overexploitation by collectors have greatly reduced the range of the species (USFWS, 2003).

The species is a small (2-15cm diameter) spineless cactus that grows to about 3 cm above the ground. Flowers of *A. asterias* are morphologically similar to those of many other North American cacti: they are moderately large (3-5cm in diameter) and bowl-shaped with the style and stigmatic lobes extending above the numerous stamens (Grant and Grant, 1979a, 1979b; Grant et al., 1979; Breckenridge and Miller, 1982). The flowers are yellow with red or orange centers. Synchronous flowering episodes occur in the spring with individual flowers opening for 1-2 days. Peak flowering typically occurs in late March – April, though some sporadic flowering may also occur during the summer months, likely in response to rainfall (Strong, 2005). Fruits are grayish red with a covering of wooly hairs, are up to 1.25 cm long at maturity (USFWS, 2003), and contain up to 202 seeds (pers. observ.). Fruits are indehiscent, but disintegrate basally dropping the seeds on or very near the mother plant. The seeds are 2.5 mm in diameter and are hat-shaped with an enlarged collar surrounding the sunken hilum. This shape has been interpreted as a possible adaptation for dispersal by water (Bregman, 1988).

Breeding experiments demonstrate that *A. asterias* is incapable of producing fruit when self pollinated (Strong and Williamson, 2007). Thus, *A. asterias* is an obligate outcrosser and all seed set is the result of pollen transferred between plants by insect pollinators. While some cacti primarily reproduce vegetatively (Mandujano et al., 1996), star cactus does not appear to exhibit asexual reproduction, thus population growth

depends on pollinator-facilitated production of offspring via sexual reproduction. Comparisons of naturally pollinated versus pollen supplemented flowers on the same plants indicate that star cactus is pollen limited (Strong, 2005). Naturally pollinated plants exhibit both lower rates of fruit set and fewer seeds per fruit compared to pollen supplemented flowers.

Pollination systems have traditionally been considered generalized when flowers are visited by multiple species, but such systems may be more specialized than they appear if only a subset of the floral visitors is effective at causing pollination (Lindsey, 1984; Schemske and Horvitz, 1984; Ollerton, 1996; McIntosh, 2005). Grant and Grant (1979*a*, 1979*b*) considered cactus flowers of the large bowl-shaped class to be most effectively pollinated by medium-large bees (*Diadasia* spp., *Melissodes* spp., *Lithurge* spp., etc.), because they carry copious pollen on their bodies and regularly contact the stigma when landing on a flower. In contrast, smaller bees (*Perdita* (*Macrotera*) spp., *Lasioglossum* (*Dialictus*) spp.) were common visitors, but were considered less effective pollinators from the observation that they were less likely to contact the stigma upon landing, while beetles (*Acmaeodera* spp., *Carpophilus* spp., *Euphoria* spp.) tended to show little interfloral movement (Grant and Grant, 1979*a*, 1979*b*; Grant et al., 1979; Parfitt and Pickett, 1980; McFarland et al., 1989; Mandujano et al., 1996). Flies (particularly Bombyliidae) have occasionally been reported to visit cactus flowers (Johnson, 1992; McIntosh, 2005; Strong, 2005), but they have not been considered as potential pollinators most likely because they do not fit the “bee pollination syndrome” proposed by earlier investigators (Grant and Grant, 1979*a*, 1979*b*; Grant et al., 1979; Grant and Hurd, 1979).

Several species of both medium-large and small bees have been found to be specialists on the pollen of cacti (Linsley and MacSwain, 1958; Grant and Hurd, 1979; Neff and Danforth, 1991; Sipes and Tepedino, 2005). While previous authors used behavioral observations to imply differences in pollination abilities among species visiting cactus flowers, McIntosh (2005) used a more direct approach to quantify pollinator effectiveness by comparing differences among flower visiting species in their abilities to affect seed set. Effective pollinators can be defined as those species that produce a relatively large number of seeds per visit, while ineffective pollinators are those that produce relatively few or no seeds per visit. By exposing virgin flowers to single pollinator visits and then counting the number of seeds produced per fruit, McIntosh found that three species of medium-sized cactus-specialist bees were the most effective pollinators of two species of *Ferocactus*. Preliminary observations (Strong, 2005) indicate that *A. asterias* flowers are visited by one species of ant, one species of fly, six species of beetle, and at least 12 bee species, including some bee species known to be cactus-specialists. Strong (2005) also reported that bee visitors were more likely than beetles to contact the stigmas of *A. asterias* flowers.

Pollinator species often vary significantly in effectiveness due to differences in behavioral and/or morphological characteristics (Schemske and Horvitz, 1984; Johnson, 1992; Olsen, 1997; McIntosh, 2005). The term “pollinator effectiveness” has been used by various investigators with different meanings including effectiveness in: 1) removing pollen from a flower, 2) depositing pollen on the stigma, and 3) causing fruit and/or seed set (Motten et al., 1981; Young, 1988; Inouye et al., 1994). For the purposes of this study, I am defining effectiveness as the number and/or percent of seeds set per pollinator

visit, because this is a direct way to measure each pollinator's effect on plant fecundity (Spears, 1983; Young, 1988; Olsen, 1997).

The "importance" of individual pollinator species can be measured as the product of effectiveness and visitation frequency (Lindsey, 1984; Young, 1988; Olsen, 1997). The importance of a given pollinator can vary spatially (over the plant's geographic range) and temporally (within and between flowering seasons) due to fluctuations in pollinator abundance or rate of visitation (Pettersson, 1991; Fishbein and Venable, 1996; Gomez and Zamora, 1999; Wall et al., 2003; Wiggam and Ferguson, 2005), which may be affected by plant community composition.

The recovery plan for *A. asterias* (USFWS, 2003) calls for studies that measure rates of gene flow within and among known localities. Such gene flow is the result of either seed dispersal or pollen dispersal. Both seed dispersal and pollen dispersal are difficult to assess directly in the field, however pollen dispersal parameters can be estimated by either measuring the distribution (mean, variance, kurtosis) of pollinator flight distances between plants (Levin and Kerster, 1968; Levin and Kerster, 1969a, 1969b; Schaal, 1980; Schmitt, 1980; Fenster, 1991) or by tracking the movement of pollen analogues such as dyes (Campbell, 1985; Campbell and Waser, 1989; Talavera et al., 2001). Several investigators (Stockhouse, 1976; Waser and Price, 1982; Waser, 1988; Fenster et al., 1996) have found fluorescent dyes to provide a reasonable estimate of pollen flow in that the dye dispersal follows a similar distribution compared to pollen. With the dispersal parameters obtained from dyes, one can then use Wright's neighborhood model (1943, 1946, 1969) to calculate genetic neighborhood size and area. A genetic neighborhood is the portion of a population in which mating can be assumed to

occur at random so that all individuals in the same neighborhood have an equal probability of mating with each other. Neighborhood size is the number of individuals within a genetic neighborhood, and neighborhood area is the geographic area that such a neighborhood encompasses. If genetic neighborhood size/area were as large as or larger than a local patch of individuals, gene flow within that patch would be considered extensive, as the patch would represent a panmictic population of randomly mating individuals. On the other hand, if neighborhood size/area were smaller than a local patch, this would indicate a restriction of gene flow and a subsequent level of population subdivision within the local patch.

Numerous ecological factors potentially affect pollen dispersal and thus gene flow in plants. For example, pollen dispersal distances may vary greatly among pollinator species foraging on the same plant species (Schmitt, 1980) and the density of flowers in a plant population is negatively correlated with pollen dispersal distances (Levin and Kerster, 1969*a*, 1969*b*; Fenster, 1991). Other studies (Campbell, 1985; Caruso, 1999) have shown that the co-occurrence of other species of flowering plants can reduce pollen dispersal to conspecific flowers through competition for pollinators. However, the relationship between species that share pollinators is not necessarily antagonistic, and in some cases co-flowering species may even facilitate pollen flow (Geer et al., 1995; Moeller, 2004).

The purpose of this study is to: (1) determine the effectiveness and importance of various floral visitors to the pollination of *A. asterias*, and (2) estimate pollen dispersal within a population of *A. asterias*. The following questions were addressed: (1) Do floral visitors differ in their effectiveness in causing pollination and what characteristics of

pollinators are correlated with effectiveness? (2) What are the visitation frequencies of various insect species to flowers of *A. asterias*? And (3) based on their visitation frequency and pollinator effectiveness, which pollinators are most important to the pollination of *A. asterias*? The answers to these questions will be used to inform management officials working to recover *A. asterias*.

II. MATERIALS AND METHODS

Study Site—The study was conducted on a ~1.9 hectare portion of a privately owned ranch in Starr County, Texas. The vegetational community at the site is typical of Tamaulipan thornscrub consisting of *Acacia rigidula*, *Prosopis glandulosa*, *Opuntia leptocaulis*, *Varilla texana*, *Opuntia engelmannii* var. *lindheimeri*, *Castela texana* and a number of other less abundant spiny shrubs. The study site contains a diverse array of cactus species including *O. leptocaulis*, *O. engelmannii* var. *lindheimeri*, *Echinocereus enneacanthus*, *Thelocactus bicolor*, *A. asterias*, *Ferocactus setispinus*, *Mammillaria heyderi*, *Echinocereus reichenbachii* var. *fitchii*, *Echinocactus texensis*, *Echinocereus pentalophus*, *Mammillaria sphaerica*, *Opuntia schottii*, *Coryphantha robertii*, *Lophophora williamsii* and *Wilcoxia poselgeri*. The number of *A. asterias* individuals at the study site is approximately 1,146 (G. K. Janssen, 2007, pers. comm.), and the average density of individuals at the site is approximately 445/ha. (A. W. Ferguson, 2007, pers. comm.).

Pollinator Effectiveness—Pollinator effectiveness was measured to determine which floral visitors most successfully pollinate *A. asterias*. Plants were chosen haphazardly throughout the population to avoid the clustering of bagged, unavailable flowers in one area which could potentially affect pollinator foraging behavior. Approximately 10% of the plants blooming on a given day were used for effectiveness trials. These plants ($n = 73$) were covered with a fine mesh bag prior to anthesis. On the

day of flowering, bags were removed one at a time, and each flower was observed until it had been visited by an insect. Trained observers recorded the following variables for each observation: (1) species of the visitor, (2) date, (3) time of day, (4) duration of visit, (5) contact or no contact with the stigma, (6) landed on or did not land on the stigma when entering the flower. Variable 6 refers to a specific type of stigma contact by floral visitors, while variable 5 refers to any type of stigma contact. Once the insect had left the flower, the plant was re-covered with the mesh bag to prevent further pollination events. Additionally, the plants were covered with metal cages to prevent the herbivory of floral parts during fruit maturation. Once the fruits ($n = 12$) had matured, they were collected and the number of seeds for each fruit was recorded. When possible, the number of unfertilized ovules for each fruit was also recorded and percent seed set was determined as the number of seeds/total number of ovules for each fruit. Natural levels of fruit set and seed set were observed for open-pollinated control plants ($n = 97$) in order to determine the reproductive output of *A. asterias* under natural conditions and to provide a control with which to compare the effectiveness of various pollinators. These control plants were chosen in the same manner as plants in the effectiveness trials and they represented approximately 10% of the flowering individuals from each bloom period, though they were not caged in the same manner as treatment plants in order to avoid exclusion of pollinators in the event that their flowers reopened the following day.

Pollinator effectiveness of each visiting insect species was calculated as the average seed set per visit (and percent seed set when possible) by each species. Mann-Whitney U tests were used to test the hypothesis that species differed from each other and from open-pollinated controls in their effectiveness at causing seed set. Additionally,

tests of the difference between two proportions were used to determine whether or not visiting species differed from each other and from the open-pollinated controls in their ability to affect fruit set. Uncommon species and those whose visits did not result in fruit set were excluded from these analyses.

Effectiveness of visiting species at causing fruit set was compared to each species' (1) mean visit duration and (2) proportion of visits in which the visitor landed on the stigma using correlation analyses (Pearson's Correlation Coefficient). I predicted that visit duration would be negatively correlated with effectiveness, because visitors spending long periods of time in individual flowers would exhibit less inter-floral movement than visitors that spent less time foraging on each flower. Such inter-floral movement is required for effective pollination in *A. asterias*, because it is a self-incompatible species. I also predicted that there would be a positive correlation between visitors landing on the stigma and effectiveness. Visitors landing on the stigma should be effective pollinators because they would potentially be covered with heterospecific pollen rather than self pollen when they contact the stigma. The ant *Forelius mccooki* was excluded from this second analysis, because they could not be said to land on the stigma since they did not approach the flowers from the air as other visitor species did.

Pollinator Importance—Visitation frequencies of species were calculated as the total number of visits by each species divided by the total number of observation hours from the effectiveness study (20.78 hours). Pollinator importance was determined for visiting species by multiplying the effectiveness of a species (average seed set/visit) by its respective visitation frequency.

Pollen Dispersal—Fluorescent powder dye was used as a pollen analogue to estimate pollen dispersal distances within the study population. Source plants were chosen haphazardly throughout the population to avoid overlap of dispersal distributions. During each bloom period, powder dye was liberally applied to the anthers of 1-3 star cactus flowers with a paintbrush using a different color of dye for each flower. Dye was applied shortly after anthesis. Between 24-48 hours after flowering, the stigmas of all *A. asterias* flowers (excluding the source flowers and the treatment and control flowers from the effectiveness study) in the study area were collected and stored in individual containers. Additionally, stigmas were collected from the flowers of all other species of cacti in the study area that were open during this experiment in order to determine whether or not individual pollinators visited multiple species. All stigmas were then observed in the laboratory under a microscope to determine which flowers received dye particles. The number of dye particles per stigma could not be reliably counted because dye particles tended to clump so stigmas were simply scored for the presence or absence of dye. The distance between donor flowers and all recipient flowers was then measured in the field. Estimates of genetic neighborhood size, area, and diameter were then calculated based on the axial variances of dispersal distances, the kurtosis of the distribution, and the density of *A. asterias* individuals in the study population according to the methods provided by Wright (1969). The formula for neighborhood size (N_e) calculated from pollen dispersal distances is ...

$$N_e = m \pi s^2 d / 2$$

where d (445 individuals/ha) is the density of individuals, s^2 is the axial variance of dispersal distances, and m is the multiplier of Wright (1943, 1946) adjusted for kurtosis according to Wright (1969). The formula for neighborhood area (A) is ...

$$A = Ne / d$$

where d again is the density of individuals, and neighborhood diameter (D) is ...

$$D = \sqrt{(A/\pi) * 2}.$$

III. RESULTS

Pollinator Effectiveness—In this study, there were eight species of floral visitors including at least four species of bee (three species of *Ashmeadiella* were lumped together due to difficulty distinguishing between them in the field), one ant species, one fly species, and two species of beetle (Table 1). However, only two species (*Diadasia rinconis*, *Macrotera lobata*) visited often enough to statistically analyze their pollinator effectiveness.

Visits from the bee *D. rinconis* ($n = 10$) were found to be more effective in causing fruit set (95% C.I. of difference between proportions = 0.63 ± 0.30) than those from the bee *M. lobata* ($n = 41$) (Figure 1). *Diadasia rinconis* was also more effective than *M. lobata* in terms of seed set per visit ($U = 66, p < 0.001$) (Figure 2). Single visits to flowers by *Diadasia rinconis* did not differ significantly from open-pollinated controls in terms of fruit set (95% C.I. of difference between proportions = 0.09 ± 0.30) (Figure 1), seed set ($U = 377.5, p = 0.450$) (Figure 2), or percentage seed set per fruit ($U = 163, p = 0.483$) (Figure 3). Visits from *M. lobata* showed significantly lower rates of fruit set (95% C.I. of difference between proportions = 0.54 ± 0.13) (Figure 1) and seed set ($U = 2762.5, p < 0.001$) (Figure 2) than controls.

Only one visit by a species of *Ashmeadiella* ($n = 6$) resulted in fruit set (Table 2). More visits would be needed to determine the effectiveness of *Ashmeadiella* spp. relative to other pollinators. None of the visits ($n = 4$) from the small bee *Dialictus* sp. resulted in

fruit set and so it is not considered to be an effective pollinator. *Dialictus* individuals never landed on the stigma when entering flowers (Table 1) and only contacted the stigma briefly (while leaving the flower) in two of their four visits.

Visits from beetles (*Acmaeodera* sp. $n = 3$, and *Carpophilus* sp. $n = 2$) and ants (*Forelius mccooki* $n = 5$) did not result in fruit set and the behavior of these visitors suggests that they are not effective pollinators of *A. asterias*. Both the beetles and ants showed little inter-floral movement, and the beetles were not observed to contact the stigma of *A. asterias* flowers when visiting flowers. However, one visit from the bombyliid fly *Anthrax irroratus* ssp. *irroratus* ($n = 2$ visits) resulted in a fruit with 129 seeds.

Fruit set was not correlated with visit duration among insect species ($r = -0.43$, $p = 0.291$, $n = 8$). However, there was a strong positive correlation between fruit set and the proportion of visits in which a visitor landed on the stigma when entering the flower ($r = 0.94$, $p = 0.002$, $n = 7$). Thus, whether or not a visitor lands on the stigma is a more reliable predictor of effectiveness than visit duration.

Pollinator Importance—*Macrotera lobata*, had the highest visitation rate of any floral visitor (Table 2), but because of its low effectiveness, it is not considered the most important pollinator of *A. asterias*. Instead, the most important pollinator appears to be *D. rinconis*, despite having a lower visitation frequency (Table 2). Bees in the genus *Ashmeadiella* were relatively uncommon visitors in this study, but showed the potential to be effective pollinators and should thus be considered to have some limited importance to the pollination of *A. asterias* (Table 2). The bombyliid fly *A. irroratus* ssp. *irroratus*, was likewise a rare, but somewhat effective pollinator,

and like *Ashmeadiella* spp. should be considered to have some importance as a pollinator (Table 2).

Dialictus sp. was both an infrequent and ineffective visitor and thus should not be considered an important pollinator of *A. asterias*. Similarly, *Acmaeodera* sp., *Carpophilus* sp., and *F. mccookii* were neither frequent visitors nor effective pollinators and should not be considered important to the pollination of *A. asterias*.

Pollen Dispersal—The dispersal of fluorescent dye particles followed a leptokurtic distribution with a mean dispersal distance of 25.1m from source plants and an axially corrected variance of 153.2m. There were a total of 13 source plants and 69 recipient plants (*A. asterias*). Approximately 80% of all recipient plants were located within 30m of the source plant (Figures 4, 5). The longest dispersal event recorded was 142.2m. There were also dispersal events in which dye was transferred from the *A. asterias* source plant to the stigma of another cactus species (*Echinocereus reichenbachii* ssp. *fitchii* ($n = 2$), *Echinocereus enneacanthus* ($n = 2$), *Thelocactus bicolor* ($n = 1$)).

Genetic neighborhood area adjusted for kurtosis was 938.5m^2 (0.094ha). Neighborhood size was 41.8 individuals with a 95% C.I. of 26.6 – 56.9 individuals. Neighborhood diameter calculated from the estimate of neighborhood area was 34.6m.

TABLES

Table 1—Insect species visiting *Astrophytum asterias* flowers for effectiveness trials in 2006-2007. Qualitative variables relating to each species' visitation behavior are included.

Visitor Species	Stigma Contact (%)	Landed on Stigma (%)	Visit Duration (sec)	Visits (#)
<i>Acmaeodera</i> sp. (Coleoptera: Buprestidae)	0	0	>600	3
<i>Anthrax irroratus</i> (Diptera: Bombyliidae)	100	100	76.00	2
<i>Ashmeadiella</i> spp. (Hymenoptera: Megachilidae)	83.33	33.33	30.80	6
<i>Carpophilus</i> sp. (Coleoptera: Nitidulidae)	0	0	>600	2
<i>Diadasia rinconis</i> (Hymenoptera: Apidae)	100	80	29.20	10
<i>Dialictus</i> sp. (Hymenoptera: Halictidae)	50	0	54.00	4
<i>Forelius mccooki</i> (Hymenoptera: Formicidae)	80	0	43.20	5
<i>Macrotera lobata</i> (Hymenoptera: Andrenidae)	73.17	9.76	66.42	41

Table 2—Percent fruit set, seed set, visitation rates, relative visitation frequencies, and pollinator importance of visitors to *Astrophytum asterias*.

Visitor Species	Fruit Set (%)	Number of Seeds/Visit	Seed Set/Fruit (%)	Visits/Hour	Relative Visitation Frequency	Pollinator Importance
<i>Acmaeodera</i> sp.	0	0	0	0.14	0.04	0
<i>Anthrax irroratus</i>	50	64.50	?	0.10	0.03	6.19
<i>Ashmeadiella</i> spp.	16.67	8.17	89.09	0.29	0.08	2.36
<i>Carpophilus</i> sp.	0	0	0	0.10	0.03	0
<i>Diadasia rinconis</i>	70	60.70	75.94	0.48	0.14	29.20
<i>Dialictus</i> sp.	0	0	0	0.19	0.05	0
<i>Forelius mccooki</i>	0	0	0	0.24	0.07	0
<i>Macrotera lobata</i>	7.32	1.37	22.27	1.97	0.56	2.69
Control	60.82	50.07	74.84			

FIGURES

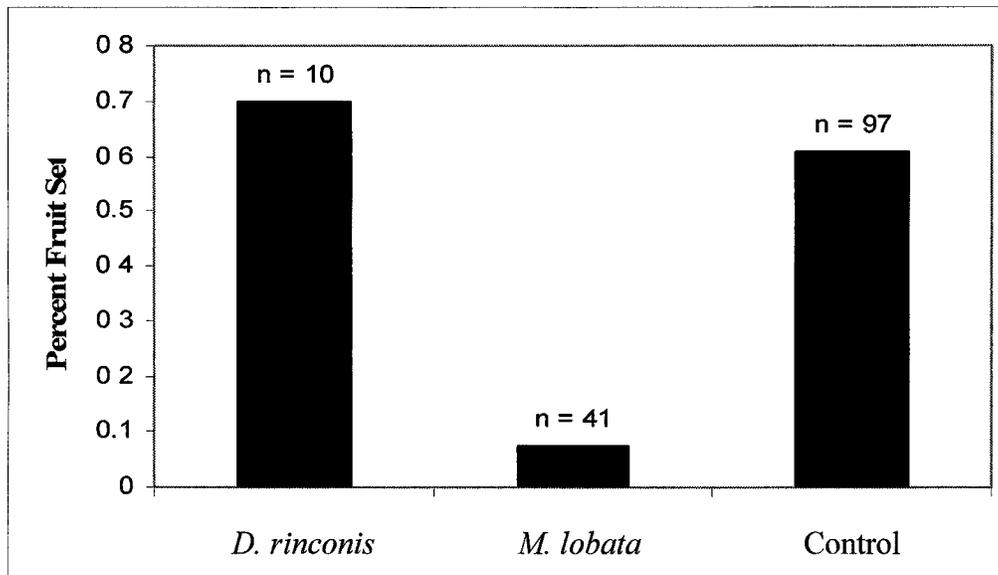


Figure 1—Percent fruit set by the two most abundant visitors to *Astrophytum asterias* compared to the open-pollinated controls.

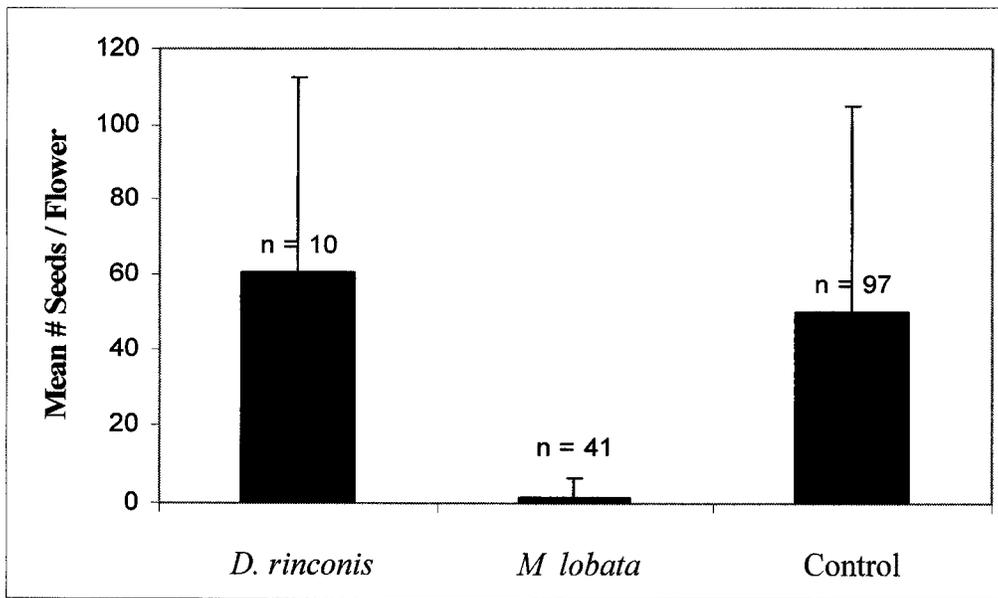


Figure 2—Percent fruit set by the two most abundant visitors to *Astrophytum asterias* compared to the open-pollinated controls. Error bars indicate 1 SD.

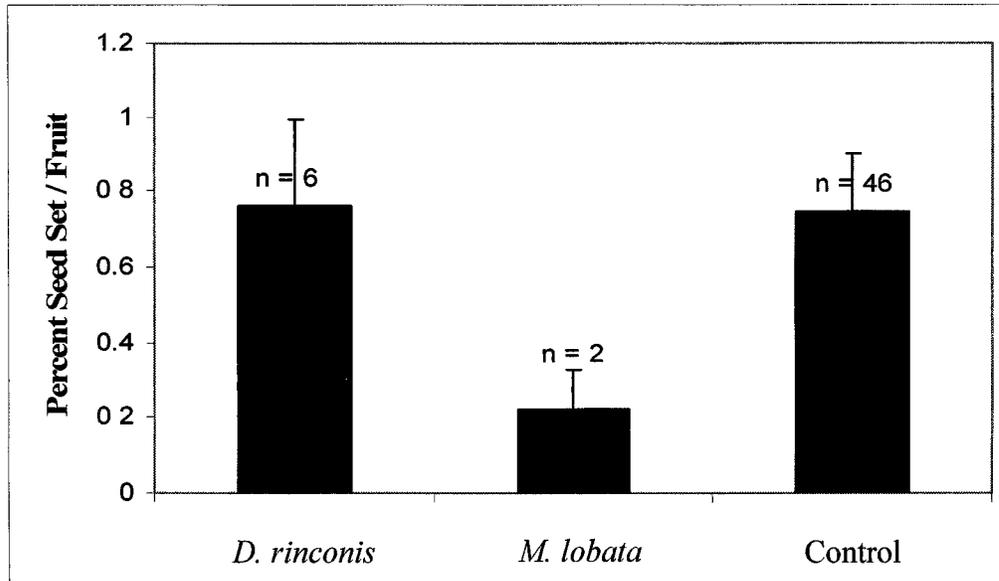


Figure 3—Mean percent seed set per fruit for the two most abundant visitors to *Astrophytum asterias* compared to open-pollinated controls. Error bars indicate 1 SD.

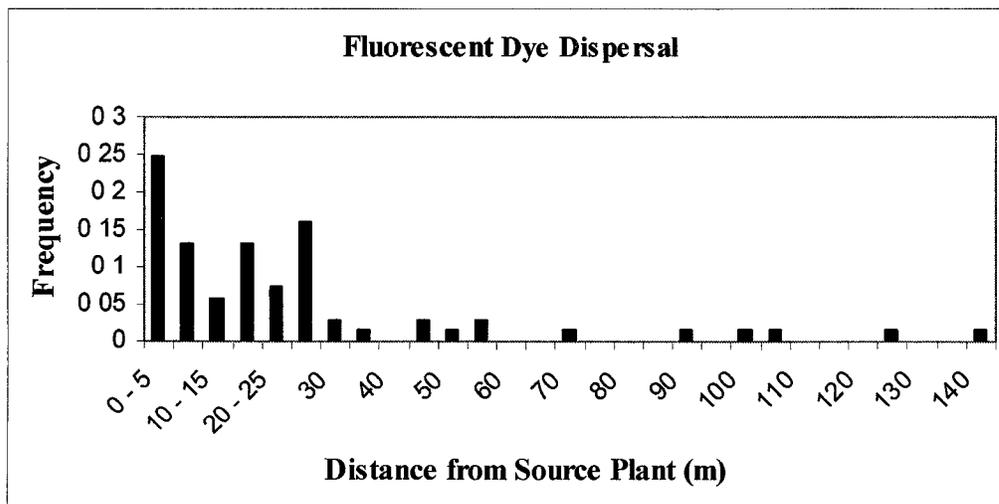


Figure 4—Frequency distribution of fluorescent dye dispersal distances.

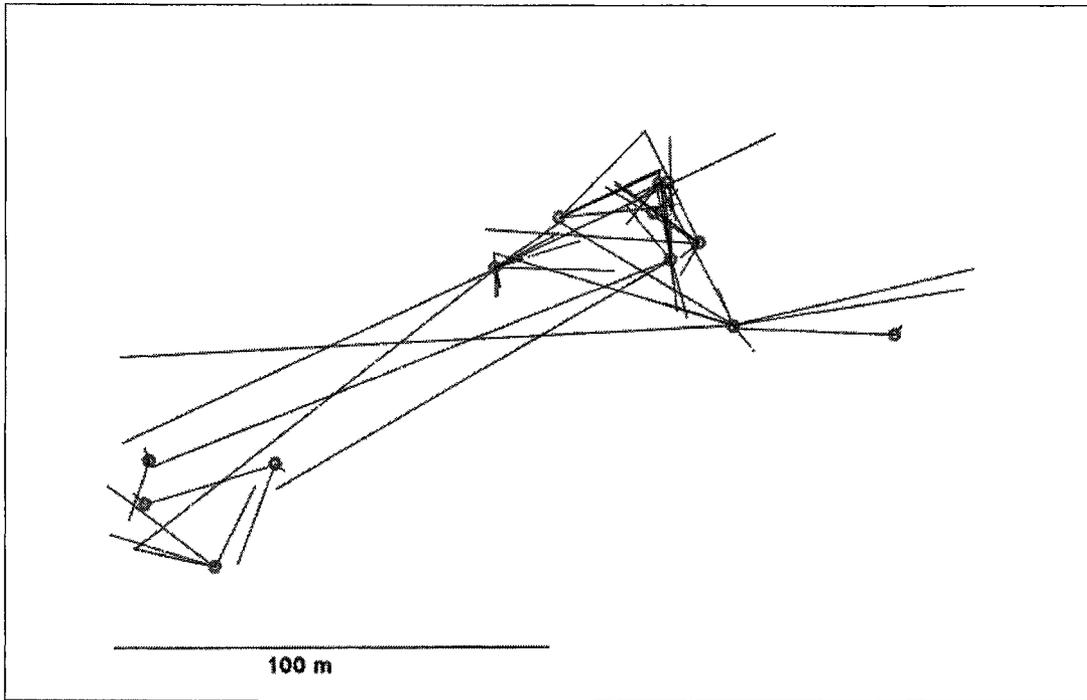


Figure 5—Visual representation of fluorescent dye dispersal within the study patch of *Astrophytum asterias*. Circles represent source plants and lines represent dispersal events to recipient plants.

IV. DISCUSSION

Pollinator Effectiveness and Pollinator Importance—The composition of floral visitors to *A. asterias* includes multiple species from diverse pollinator guilds (small bees, larger bees, beetles, ants, flies) so that one might initially conclude that it represents a very generalized pollination system. However, because only a small number of these visiting species is able to affect seed set (and only one species appears to be highly effective), the pollination system of *A. asterias* should be considered more specialized. A similar pattern of specialization can be seen with the cacti *Ferocactus cylindraceus* and *F. wislizeni* (McIntosh, 2005) in which three bee species (*D. rinconis*, *Ashmeadiella opuntiae*, *Svastra duplocincta*) carry out virtually all of the pollination services, despite the occurrence of multiple other floral visitors.

The results of this study suggest that *D. rinconis* is the most effective pollinator of star cactus. Also, even though it visits less frequently than some other visitors (i.e. *M. lobata*), *D. rinconis* appears to be the most important pollinator in this system, which means that it is responsible for the greatest portion of seed set in a given population. A single visit from *D. rinconis* resulted in levels of seed set equivalent to controls, which may have received multiple pollinator visits. McIntosh (2005) also found *D. rinconis* to be the most effective pollinator (higher fruit set percentage, more seed produced per visit) of two other cacti; *F. cylindraceus* and *F. wislizeni*.

The data presented in this study show that despite being the most frequent floral visitors, *M. lobata* individuals are not very effective pollinators. However, because of their high visitation frequency, these bees are likely responsible for a small portion of the total seed set in a given population. Other bee species (*Ashmeadiella* spp. in particular) and the bombyliid fly *A. irroratus* may also contribute to the pollination of star cactus but it is difficult to determine the extent of their importance from the limited number of visits and the small number of fruits set ($n = 2$) by these species in this study. Consistent with the results reported here, McIntosh (2005) found that *Ashmeadiella opuntiae* was a less effective pollinator (lower fruit set percentage, fewer seeds produced/visit) of *F. cylindraceus* and *F. wislizeni* than *D. rinconis*, but she concluded that it still contributed to the pollination services of those cacti. Also, this study represents the first documented case of a fly (*A. irroratus*) successfully pollinating a cactus flower, which highlights the necessity of empirically evaluating the effectiveness of all visiting species; even those that do not conform to the expectations of pollination syndromes (Mayfield et al., 2001).

It seems unlikely that the two beetle species (*Acmaeodera* sp., *Carpophilus* sp.) and ants (*F. mccoeki*) observed visiting *A. asterias* flowers in this study are important to the pollination of star cactus. The beetles were never observed to contact the stigma and individuals tended to remain in a single flower for long periods of time (>10min.) rather than moving among flowers. While the ants often contacted the stigmas of flowers, none of their visits resulted in fruit set. Ants have in general been considered to be poor pollinators because they secrete antibiotic substances that inhibit pollen function (Beattie et al., 1984).

One important trait of pollinators that was not examined in this study was possible differences in foraging range between species. Species that forage over a larger area would

likely disperse pollen over a larger area as well, assuming they are effective pollinators. Gathmann and Tschamntke (2002) found a positive correlation between body size and foraging range in solitary bees. This might indicate that the larger pollinators of *A. asterias* (i.e. *D. rinconis*, *Ashmeadiella* spp.) would be better long-distance pollen dispersers than smaller species (i.e. *M. lobata*, *Dialictus* sp.).

Pollen dispersal—The estimate for neighborhood area (~0.094ha.) calculated for the study population of *A. asterias* is much smaller than the spatial dimensions of the entire patch (~0.094ha.). Correspondingly, the estimate for neighborhood size (~27 – 57 individuals) is considerably smaller than the estimated total number of *A. asterias* (~1146 individuals) in the study patch. These neighborhood metrics suggest that most pollen dispersal occurs within smaller subunits within the larger geographically defined patch. However, there is also evidence that pollen is rarely dispersed across the extent of the study site.

There are a number of reasons to believe that the estimates of neighborhood size and area calculated in this study are somewhat conservative. First of all, due to logistical constraints, no attempt was made in this study to measure pollen flow between star cactus localities. Known patches of *A. asterias* in Starr County are separated from each other by distances ranging from 0.45 – 10.33km (Terry, 2005). A larger-scale dispersal study would need to be carried out to determine whether or not pollen is dispersed between such geographically separated patches. If dye/pollen was found to be dispersed among sites, the resulting estimates of neighborhood size and area would be greatly increased. McDonald and McPherson (2005) report that *D. rinconis* individuals are capable of transferring pollen analogues nearly 1 km while foraging on Pima Pineapple Cactus (*Coryphantha scheeri* var. *robustispina*). If *D. rinconis* individuals foraged over that great of a distance when visiting

A. asterias, it would be possible for pollen to be carried between geographically distinct localities, many of which are separated by less than 1km.

Additionally, this study only attempted to estimate gene flow as it relates to pollen dispersal. Seed dispersal also has the potential to affect gene flow, and long distance seed dispersal would increase estimates of neighborhood area and size. Little is known about the dispersal of *A. asterias* seeds (USFWS, 2003).

The most common form of seed dispersal in the Cactaceae appears to be endozoochory (Bregman, 1988) in which animals eat the fleshy fruits and deposit their seeds at a new site within their feces. Seeds can be dispersed great distances in this manner, potentially leading to extensive gene flow. This type of dispersal is particularly common in species of *Opuntia* and in columnar cacti (Montiel and Montana, 2000; Godinez-Alvarez et al., 2002). The fruits of *A. asterias* are not large and fleshy and have not been observed to be eaten by birds or mammals. Instead, their seeds simply fall onto or very near the mother plant as the basal portion of the fruit disintegrates (USFWS 2003). Seedlings can often be found clustered within a few centimeters of what appears to be a lone mother plant (pers. observ.), which would seem to indicate very limited seed dispersal. Friedman and Stein (1980) suggested that limited seed dispersal may be beneficial in harsh landscapes where resources are patchy so that the offspring remain in the favorable micro-habitat of the parent plant. However, such limited dispersal may also have negative consequences such as the overcrowding of individuals in a suitable habitat patch resulting in resource competition or the clustering of genetically similar individuals (Venable and Brown, 1993), which in the case of self-incompatible species could reduce the number of compatible mating types within a patch.

Bregman (1988) considers seeds of plants in the genus *Astrophytum* to be adapted to dispersal by water (hydrochory). When these seeds are dropped into water, the expanded collar around the sunken hilum forms a cup that retains an air bubble, serving as a flotation device for the seed. In a test of seed buoyancy, Bregman (1988) noted that seeds of *Matucana pujupatii* (which are very similar morphologically to those of *Astrophytum* spp.) continued to float 24 hours after being placed in water while the seeds of many other cactus species sank almost immediately. It seems possible that at least some star cactus seeds could be carried away to distant sites by water during periodic heavy rainfall events. If this is the case, overall gene flow for star cactus could be much greater than anticipated from pollen dispersal estimates alone.

Investigators beginning with Levin and Kerster (1969a, 1969b) have shown that floral density and pollen dispersal distances are negatively correlated such that low density patches experience pollen dispersal over greater areas than high density patches. The patch used for this study had a density of 445 individuals/ha. Other known patches of *A. asterias* contain densities of 487, 338, 248, and 150 individuals/ha (A. W. Ferguson, 2007, pers. comm.). Based on the relationship between density and dispersal, one would expect greater pollen dispersal in the three lower density patches of *A. asterias* with a subsequent increase in neighborhood area for those populations. Also, one would expect more limited pollen dispersal and subsequently smaller neighborhoods in higher density patches of *A. asterias*.

While the lack of information about seed dispersal and possible inter-patch pollen flow may cause genetic neighborhood parameters in this study to be underestimated, the measure used for patch density may cause an upward bias of neighborhood estimates.

Density at the study site and at the other four localities was measured as the total number of

A. asterias individuals located within a 1ha plot (divided into four 0.25ha subplots) that was centered within the larger patch (A. W. Ferguson, 2007, pers. comm.) at each site.

Neighborhood estimates call for the genetically effective density of individuals in a patch, which includes only the reproductive (i.e. flowering) individuals, while the density measure used in this study included both reproductive and non-reproductive (i.e. non-flowering) individuals. Because the density of individuals as measured in this study is likely to be higher than the genetically effective density because of the inclusion of non-flowering individuals, the present calculations may actually represent overestimates of neighborhood size, area, and diameter.

One ecological factor that can potentially affect pollen dispersal is competition for pollination with other simultaneously blooming species. Two of the most frequent visitors of *A. asterias* (*M. lobata*, *D. rinconis*) are also the most frequent floral visitors to co-occurring cactus species including *Coryphantha macromeris* var. *runyoni*, *E. enneacanthus*, *E. pentalophus*, *E. reichenbachii* var. *fitchii*, *F. setispinus*, *L. williamsii*, *M. sphaerica*, and *T. bicolor* (A. W. Strong, 2007, pers. comm.). This, along with the documented dispersal of fluorescent dye from *A. asterias* to some of these other species would seem to suggest the possibility of competition for pollination among cactus species.

Levin and Anderson (1970) suggest several strategies that plant species can adopt to minimize competition for pollination with other simultaneously flowering species, including differences in the seasonal and/or daily timing of anthesis. No formal study has been carried out comparing the flowering phenology of cactus species co-occurring with *A. asterias*, but personal observations from 2005-2007 indicate that *A. asterias* tends to begin flowering somewhat earlier in the season than some of the more prolific (in terms of flower production)

cactus species (i.e. *O. engelmannii* var. *lindheimeri*, *E. enneacanthus*), though there is certainly overlap between flowering seasons. In 2007, the first *A. asterias* flowering event occurred on 18-19 March, and there were four additional *A. asterias* flowering events from late March to early April before *O. engelmannii* var. *lindheimeri* and *E. enneacanthus* began flowering in mid-April (14-15 April for *E. enneacanthus*). Personal observations also indicate that *A. asterias* may sometimes avoid competition for pollination by opening their flowers later in the day than other species. On 29 April 2007, *D. rinconis* and *M. lobata* individuals were observed visiting the flowers of *O. engelmannii* var. *lindheimeri* and *E. reichenbachii* ssp. *fitchii* in the morning and early afternoon, but both of these species had ceased flowering by the time *A. asterias* flowers began opening later that afternoon (~1500 h).

The patterns of genetic structuring indicated by neighborhood estimates in this study are somewhat inconsistent with the preliminary results of population genetic data for *A. asterias* (Terry, 2005, 2007). Neighborhood estimates calculated from pollen dispersal distances suggest that gene flow is restricted such that population substructure exists within individual patches of *A. asterias*. However, Terry (2005, 2007) found that geographically isolated patches (0.45 - 10.33km) of *A. asterias* in Starr county showed only slight to moderate differentiation from each other (pair-wise F_{ST} values: 0.023 – 0.103) based on patterns of variation among five microsatellite loci. Terry (2007) also found that migration rates between patches of *A. asterias* were quite high (2.18 - 10.74 individuals/generation) which also indicates high levels of gene flow among isolated patches. These results imply much more extensive gene flow in *A. asterias* than predicted from neighborhood estimates in the present study.

Part of this discrepancy between the population genetic data and the neighborhood estimates may result from the neighborhood estimates being an underestimate of gene flow for reasons already described. However, it is also possible that results from the microsatellite data represent an overestimate of gene flow. First of all, the number of individuals available for genetic sampling was constrained by the necessity of non-invasive sampling techniques. To avoid damage to *A. asterias* individuals, sampling was restricted to floral tissue so that only mature individuals that were blooming on the sampling dates could be used (Terry, 2005). This restriction of sample size makes it less likely that genetic substructure within patches would be detected. Furthermore, this sampling technique limits the analysis to mature individuals which may be decades old, so that changes in genetic structure resulting from recent events (i.e. subdivision of larger populations due to road construction or other land alterations) may not be detectable. Additionally, the model used to calculate migration rates between patches assumes that immigration and emigration are in equilibrium. That would not be the case if the current level of isolation between patches was the result of a recent subdivision of a once more extensive population.

Clearly, more remains to be done to address questions concerning rates of gene flow within and among patches of *A. asterias*. A comprehensive approach should involve more extensive sampling of individuals for population genetic studies as well as larger-scale pollen dispersal studies. Genetic sampling should include more individuals from previously sampled patches as well as individuals from patches that have not yet been sampled. Also, if non-invasive techniques could be developed to sample immature individuals, this would greatly enhance population genetic analyses. Dispersal studies will need to be designed to detect long-range dispersal events (inter-patch pollen flow) if they occur, because of the

potential for long-range dispersal to create genetic connectance among isolated patches. The combination of these techniques should provide a much clearer picture of gene flow and population structure in *A. asterias*.

Conservation and Management Implications—Because *A. asterias* is an obligately-outcrossing plant (Strong and Williamson, 2007), it is dependent on its pollinators in order to maintain viable populations. These pollinators in turn are also dependent on their pollen sources in order to reproduce and maintain viable populations. Cactus-specialist bees such as *D. rinconis*, *M. lobata*, and *Ashmeadiella* spp. likely depend on the occurrence of multiple species of cacti blooming throughout their foraging season to provide a continuous source of pollen with which to provision their nests. Moeller (2004) provides evidence that plants can benefit reproductively from the presence of other plant species sharing the same pollinators. He found that *Clarkia xantiana xantiana* populations showed increased pollinator availability and pollen deposition rates in mixed communities containing pollinator-sharing congeners compared with communities lacking these congeners. This result in conjunction with the obligate need for pollen for bee offspring production suggests that diversity and abundance of other cacti at a given site may be needed to maintain adequate pollinator populations for *A. asterias*. Habitat loss due to range management practices is considered one of the greatest direct threats to populations of *A. asterias* in south Texas (USFWS, 2003). The common practices of root-plowing vegetation and planting pastures with non-native grasses are not only detrimental to *A. asterias* directly, but they also likely decrease the abundance and diversity of other species of cacti which may reduce habitat quality for pollinators of *A. asterias*. These practices should thus be discouraged on lands managed for star cactus.

Pollinators also have other needs that may need to be considered besides the abundance/diversity of pollen sources (Tepedino et al., 1997). The bee species in this study are solitary species (excluding the semi-social *Dialictus* sp.) that either nest in patches of bare ground (*D. rinconis*, *M. lobata*) or in hollow twigs (*Ashmeadiella* spp.). Areas set aside for *A. asterias* will need to provide adequate nesting sites for these pollinators. While natural habitat is preferable, disturbed areas such as powerline right of ways and road margins have been shown to be utilized by ground-nesting solitary bees as long as these areas are located within foraging range of floral resources (Cane and Tepedino, 2001; Russell et al., 2005).

Also, because bees are particularly sensitive to many insecticides used to control crop pests (Peach et al., 1993; Cane and Tepedino, 2001), pesticide treatments may need to be adjusted (i.e. use treatments that are less toxic to bees, spray at times when pollinators are not active) to minimize non-target effects on pollinators. Larsen et al. (2005) found that larger bees were more prone to local extinction caused by anthropogenic disturbances than smaller bees. This may be because larger species of bees require greater amounts of pollen to produce a single offspring, and thus they need more flowers on which to forage (Muller et al., 2006). If this pattern holds for pollinators of star cactus, it would mean that *D. rinconis*, the most important pollinator in the system, is the most sensitive to pollen shortages or other negative effects from human-induced disturbances. Overall, the complex network of interactions between plants, pollinators, and the surrounding landscape makes it necessary to adopt conservation measures that are ecosystem-oriented, rather than those that are simply species-oriented.

Conclusions—The bee *D. rinconis* was found to be the most effective and most important pollinator of *A. asterias*. The most frequent floral visitor, *M. lobata*, was not a

very effective pollinator, so it is of limited importance as a pollinator. Bees in the genus *Ashmeadiella* and the fly *A. irroratus* showed some ability to affect pollination, but they were infrequent visitors to *A. asterias* flowers in this study. Other floral visitors (*Acmaeodera* sp., *Carpophilus* sp., *Dialictus* sp., and *F. mcCooki*) were shown to be ineffective pollinators and they are thus not considered to be important pollinators of *A. asterias*. Neighborhood estimates calculated from dispersal distances of pollen analogues suggest that pollen flow is somewhat limited within patches. Such limited pollen flow may create a level of genetic substructure within patches, though this pattern conflicts with the preliminary results of other population genetic studies. More remains to be done to effectively address questions related to gene flow in *A. asterias*.

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