

Pollination of two species of *Ferocactus*: interactions between cactus-specialist bees and their host plants

M. E. MCINTOSH

Department of Ecology and Evolutionary Biology, 1041 E. Lowell Street; BioSciences West, Room 310, University of Arizona, Tucson, AZ 85721, USA

Summary

1. Resolving the controversy over the prevalence of generalization in plant–pollinator interactions requires field studies characterizing the pollination effectiveness of all a plant's floral visitors. Herein, the pollination effectiveness of all visitors to two species of barrel cactus (*Ferocactus*) was quantified.
2. Flowers of both species were pollinated almost exclusively by cactus-specialist bees: 99% (*F. cylindraceus* (Engelm.) Orcutt) and 94% (*F. wislizeni* (Engelm.) Britt. and Rose) of all seeds produced in this study resulted from cactus bee visits.
3. For *F. cylindraceus*, the cactus-specialist *Diadasia rinconis* was the most abundant visitor. For *F. wislizeni*, three cactus-specialists (including *D. rinconis*) plus generalists in the family Halictidae (which did not act as pollinators) each accounted for a quarter of all visits.
4. *Diadasia rinconis* visits to *F. wislizeni* flowers were more effective (per-visit) than visits by the other two cactus-specialists.
5. Pollen-collecting and nectar-collecting visits were equally effective. Nectar-collecting visits were the most abundant.
6. Apart from the non-pollinating halictids, floral visitors surprisingly did not include commonly co-occurring generalist bees.
7. These data suggest that, just as apparently specialized flowers may be visited by a diverse assemblage of generalists, so apparently generalized flowers may be visited predominantly by specialists, and that these specialists may perform virtually all of the pollination.

Key-words: Cactaceae, mutualism, specialization

Functional Ecology (2005) **19**, 727–734
doi: 10.1111/j.1365-2435.2005.00990.x

Introduction

Recent studies of plant–pollinator interactions have found visitor assemblages that are taxonomically diverse and spatially and temporally variable (e.g. Herrera 1988; Fishbein & Venable 1996). Some have argued that such generalized interactions may be the rule (Ollerton 1996; Wilson & Thomson 1996). However, only a few species of a diverse assemblage of flower visitors may actually pollinate the flowers (reviewed in Ollerton 1996; Johnson & Steiner 2000). Studies that characterize pollinator effectiveness of each member of a visitor assemblage are necessary to determine whether generalized pollination systems actually predominate. We know little of the pollination systems of many Cactaceae, plants that are abundant, widespread

and ecologically important in arid and semiarid lands of the New World.

The flowers of many cacti are visited by bees that specialize on cacti (Simpson & Neff 1987). Bees are generalized to their nectar sources, capable of visiting many kinds of plants for nectar, but many if not most bees are pollen specialists (Weislo & Cane 1996). Females visit a restricted subset of the plant species available for pollen, which they use as food for their larvae. Their preferences appear to be genetically based and unaffected by the abundance of potentially alternative floral resources available (Weislo & Cane 1996).

The relationship between the degree of a visitor's specialization to its host plant and the location of that visitor along the mutualism–antagonism continuum has been little explored in pollination research. Pollen-specialist bees might be antagonists to the plants they visit, because they actively collect and sequester pollen for larval provisions, making that pollen unavailable for pollination (Harder & Barclay 1994). They can also

be more efficient pollen harvesters than generalist bees (Strickler 1979). Conversely, pollen-specialist bees might be more likely to be mutualists than generalized visitors, because they may be adapted to the flowers they visit, and may be more abundant and predictable than other visitors (Cane & Payne 1993). Evidence to date on the relative value of specialist *vs* generalist visitors to flowers has been equivocal (Motten, Campbell & Alexander 1981; Neff & Simpson 1990; Keys, Buchmann & Smith 1995).

The behaviour of floral visitors at a given flower can be quite different depending on whether they are seeking nectar or pollen, and these differences in behaviour can affect pollinator effectiveness. Thus organizing visitors into functional groups according to the reward they seek may be a more appropriate way to categorize them than by their taxonomic affiliation (Bosch, Retana & Cerda 1997).

I studied the floral visitor assemblages of two species of barrel cacti: *Ferocactus cylindraceus* (Engelm.) Orcutt and *F. wislizeni* (Engelm.) Britt. and Rose. These plants are functionally outcrossers and have no form of vegetative reproduction, making them completely dependent on floral visitors for their reproduction (McIntosh 2002a,b). To determine the pollinator effectiveness of different visitors, the single-pollinator-visit method was used (Motten *et al.* 1981; Pellmyr & Thompson 1996), in which a single visit is allowed to each virgin flower, and the result of that visit (fruit set, seeds per fruit) is recorded. The quantity and quality components of pollinator effectiveness were estimated (Herrera 1987, 1989; Fishbein & Venable 1996), and the relative importance of different visits or visitors to the total realized fecundity of the plants was determined. Fecundity was measured as the total number of seeds produced by each group of visits or visitors (Fishbein & Venable 1996; Pellmyr & Thompson 1996). Evaluating pollinator effectiveness in terms of the total effect on fecundity is important because the effect of the quality components (e.g. fruit set or seeds per fruit) can easily be overwhelmed by the quantity component.

The questions addressed in this study were:

1. What is the taxonomic composition and relative abundances of floral visitors to *F. cylindraceus* and *F. wislizeni* at the study sites?
2. Do pollinators differ in their effectiveness?
3. Do nectar-collecting visits differ in quality from pollen-collecting visits?
4. Do visits by male bees differ in quality from visits by female bees?

Because of the generalized floral morphology of *Ferocactus* flowers (see Methods), it was expected that the visitor assemblage to these plants would be diverse in composition and variable in time. It was also expected that pollen-specialist bees would pollinate, but that they would comprise only a part of the pollinator assemblage. Finally, because different behaviours are required to

collect pollen *vs* nectar from *Ferocactus* flowers, it was expected that pollen visits would significantly differ from nectar visits in per-visit quality.

Methods and materials

STUDY ORGANISMS

The genus *Ferocactus* (Cactaceae) comprises 25–30 species, all in North America (Cota & Wallace 1997). *F. wislizeni* and *F. cylindraceus* are sister species (Cota & Wallace 1997). In the populations studied herein, *F. cylindraceus* flowered late April to September and *F. wislizeni* flowered mid-July to October. Flowering phenology, breeding system and reproductive output have been recently studied for both species at the same sites used in this study (McIntosh 2002a,b).

For both species, strong inbreeding depression limits the number of seeds produced by selfing to *c.* 2% of all seeds produced. Pollinator visitation is necessary for fruit set, and neither species reproduces vegetatively. Fruit set for open-pollinated flowers in the populations studied range from 93% to 98% of flowers for both species. Seeds per fruit for open-pollinated flowers ranged from 14 to 1727 seeds (mean = 575) for *F. cylindraceus*, and from 17 to 3064 seeds (mean = 724) for *F. wislizeni*.

The showy flowers are borne apically and are open for several days. Plants commonly open 2–3 new flowers per week and produce 30–40 flowers during a flowering season (range: 1–98 flowers for *F. cylindraceus*, 1–89 for *F. wislizeni*). Larger plants produce more flowers. The flowers of both species are large (3.8–6 cm diameter, *F. cylindraceus*; 4.5–6 cm diameter, *F. wislizeni*). They are bowl- or cup-shaped, with a short funnel-form floral tube recessed within stem tissue. The stigma is elevated above the anthers, and is often used as a landing site by visitors. The numerous stamens are tightly appressed to the style when the flower first opens, and gradually move away from the style over the 2–5 days that the flowers are open. Nectar is secreted near the base of the floral tube.

Diadasia rinconis Cockerell (Hymenoptera: Apidae) is a ground-nesting solitary bee, one of several species of *Diadasia* that specialize on cacti. Females are distinguishable from males because their abdomen is usually strongly banded, whereas abdomens of males are not. The scopae (pollen-carrying brushes composed of branched hairs) of females are also readily seen. *Diadasia rinconis* are active on cactus flowers from late March to September, and their nesting and foraging biology are moderately well known (Ordway 1987; Neff & Simpson 1992; Sipes & Wolf 2001). *Svastra duplocincta* (Cockerell) (Hymenoptera: Apidae) is also a ground-nesting cactus-specialist solitary bee (Zavortink 1975). Males are easily distinguished from females by their long antennae. *Ashmeadiella opuntiae* (Cockerell) (Hymenoptera: Megachilidae) is a smaller solitary cavity-nesting bee that is active through spring, summer and autumn, that specializes on cacti (Krombein *et al.* 1979). Differences

between sexes are more subtle in this species, and it was not usually possible to distinguish males from females.

METHODS

Single-pollinator-visit trials were conducted on *F. cylindraceus* plants at Desert Peak, a ridge 125 m high, 45 km NW of Tucson, Arizona (latitude 32°36'N, longitude 111°14' W, 640 m elevation), and on *F. wislizeni* plants at the Santa Rita Experimental Range, 40 km south of Tucson (31°54'N, 110°53'W, 914 m elevation), during the summers of 1996–98. Mesh-covered wire baskets were placed on the apex of flowering plants to exclude pollinators (mesh hole diameter ≤ 1 mm). A cover was briefly removed to allow a single pollinator to visit a virgin flower. The identity, sex and behaviour of the visitor were recorded, the visited flower was marked, and the cover was replaced. Later, the fate of the flower (formed a fruit or was aborted) was recorded, fruits were collected and seeds were counted.

A particular visitor or species was considered a 'pollinator' if any fruits resulted from any of their visits. Although single visits were primarily recorded, multiple visits (often by different taxa) to a single flower sometimes occurred inadvertently. These multiple visits were included in counts of total visits. However, because 'multiple visits' included a variety of events (several back-to-back visits by the same individual insect, two or more visits by insects of the same species but of different sexes or different visit types, multiple visits by several different taxa), and because the effects of multiple visits can be complex (e.g. a second visitor may remove some of the pollen deposited on the stigma by the first visitor), multiple visits to a single flower were not included in data analyses of pollinator quality.

Herein, 'pollinator effectiveness' refers to the combined effects of quantity and quality components on realized plant fecundity (total seeds produced). 'Quantity' was defined as number of visits recorded. Two measures of 'quality' were used (per-visit effects on the reproductive fate of a single flower): the probability of fruit set from a single visit, and the mean number of seeds per fruit resulting from a single visit (aborted fruits excluded).

The relative abundances of the different visitor taxa were determined from the number of visits observed. My protocol was to remove a cover and leave it off until a single visitor arrived. If no visitor arrived within 20 min, I replaced the cover and made another attempt later the same day or on another day. Observations were conducted between approximately 09:00 and 13:00 hours (see Discussion).

'Fruit set' is percentage of visits in a category (taxon, visit type, etc.) that resulted in a fruit. Fruit set for open-pollinated flowers in the populations studied ranged from 93% to 98% of flowers for both species (McIntosh 2002b). Also, plants did not abort more fruits early or late in their flowering periods than in the middle (McIntosh 2002a). Therefore, it is reasonable

to assume that when a flower was aborted following a single pollinator visit, it was because the visitor failed to deposit pollen that was sufficient in quality and/or quantity to set fruit.

To clarify the relationship between quantity and quality, the percentage of all visits in a category (e.g. bees of species X) was compared with the percentage of all fruits matured and the percentage of all seeds matured in that category. If visits do not differ in quality, realized fecundity is determined by the number of visits. If fruit set is greater than average in a category, then the percentage of all fruits in that category will be greater than the percentage of all visits. If mean seeds per fruit is greater than average for that category, then the percentage of all seeds will be greater than the percentage of all fruits. Total seeds produced is the product of the preceding three measures (number of visits \times mean fruit set \times mean seeds per fruit). This measure reflects the 'bottom line' impact on the plant's overall female reproductive success.

Visitors other than the three cactus-specialist bees were identified to genus or tribe, if bees, and to family for other insects. Field identifications were corroborated by collecting and identifying floral visitors. However, visitors could not always be identified to the species level.

In 1996–97, all observed visits were recorded. In 1998, visits by *Augochlorella* spp., *Lasioglossum* spp., other small to tiny bees (body length ≤ 7 mm) and small flies were not recorded.

Pollen-collecting visits were easily distinguished from nectar-gathering visits. Visitors collecting pollen walk along the tops of the stamens, but nectar-seeking visitors are forced to burrow down through the stamens head first until their tongue can reach the nectaries at the base of the floral tube. Visit type was coded as: (1) *brief visits* – the visitor did not collect any floral rewards; these included brief landings, motionless perching and walking in the flower; (2) *nectar-collecting visits* – the visitor burrowed down between the stamens to reach the nectar at the base of the floral tube; (3) *pollen-collecting visits* – the visitor 'swam' along the tops of the stamens, gathering and passing pollen to the scopae; (4) *nectar- and pollen-collecting visits* – a visitor collected both nectar and pollen in one visit. In a few cases ($N = 43$ out of 519 total visits recorded) visit type was not easily categorized; these visits were excluded from the analyses involving visit type.

DATA ANALYSES

All statistical tests were performed with JMP 5.1 ® software (SAS Institute 1989–2002). Owing to sample sizes, statistical tests were performed only on data resulting from visits by the three cactus bee species. Data were pooled across years to increase sample size. For tests involving bee sex, only data from visits by *D. rinconis* and *S. duplocincta* were used. Independent factors were: the species and sex of the visitor, and the

Table 1. Composition of floral visitor taxa, by number of visits (relative abundance), 1996–98. Bold taxa are pollinators (see Methods). Taxa in *italics* are cactus specialists. Visits by some non-pollinating taxa were not recorded in 1998 ('nr'). Differences in total visits recorded among years/plant species reflect differences in sampling effort, not visitation rates. Total visits are more than those shown in other figures and tables because this table includes multiple visits to single flowers and fruits that were destroyed by predaceous Lepidoptera. 'F.cyl' = *F. cylindraceus*, 'F.wis' = *F. wislizeni*. Bee taxa are ordered as in Michener (2000)

Floral visitors <i>N</i> = total visits recorded	<i>F.cyl</i> 1996 <i>N</i> = 36	<i>F.cyl</i> 1997 <i>N</i> = 91	<i>F.cyl</i> 1998 <i>N</i> = 127	<i>F.wis</i> 1996 <i>N</i> = 35	<i>F.wis</i> 1997 <i>N</i> = 144	<i>F.wis</i> 1998 <i>N</i> = 192
<i>Bees Halictidae</i>						
<i>Halictus</i> spp. (<i>N</i> = 2)	0	0	0	0	2	0
<i>Lasioglossum</i> spp. (<i>N</i> = 14)	0	2	nr	3	9	nr
<i>Augochlorella</i> spp. (<i>N</i> = 41)	1	0	nr	4	36	nr
<i>Bees Megachilidae</i>						
<i>Ashmeadiella opuntiae</i> (<i>N</i> = 104)	0	6	0	8	28	62
Anthidiinae (<i>N</i> = 2)	2	0	0	0	0	0
<i>Megachile</i> spp. (<i>N</i> = 10)	1	0	0	0	3	6
<i>Bees Apidae</i>						
<i>Diadasia rinconis</i> (<i>N</i> = 307)	25	70	113	2	36	61
<i>Svastra duplocincta</i> (<i>N</i> = 124)	1	4	14	18	29	58
<i>Apis mellifera</i> (<i>N</i> = 5)	0	1	0	0	0	4
Unidentified large bees (<i>N</i> = 3)	0	2	0	0	0	1
Unidentified small bees (<i>N</i> = 1)	0	1	nr	0	0	nr
Other: Diptera (<i>N</i> = 6)	6	0	0	0	0	nr
Other: Lepidoptera (<i>N</i> = 1)	0	0	0	0	1	nr

type of visit. The dependent factors were fruit set (categorical data) and seeds per fruit.

To test the hypotheses that bee species or visit type (independent factors) affected fruit set, either a nominal logistic fit model test (two factors) or a likelihood ratio chi-square test (single factor) was used.

Because data transformations failed to normalize the seed counts and because of unequal variances in the seed data, non-parametric tests were used to test effects on seeds per fruit. To test the hypotheses that bee species or visit type affected seeds per fruit, a Wilcoxon/Kruskal–Wallis rank sum test was used on each independent factor. In the case of significant effects, a post-hoc Tukey–Kramer HSD test was performed for multiple comparisons to determine the significantly different categories.

A likelihood ratio chi-square test was used to test the hypothesis that bee sex affected fruit set, and Wilcoxon/Kruskal–Wallis rank sum tests were used to test the hypothesis that bee sex affected seeds per fruit (separate test for each bee species).

Although the identity of individual plants is likely to affect fruit set and seeds per fruit (McIntosh 2002b), these effects could not be factored out in these data, because there were not enough replicates per individual plant.

Results

For both *Ferocactus* species, pollinating visitors were three cactus bees (*D. rinconis*, *S. duplocincta* and *A. opuntiae*), *Megachile* spp. and *Halictus* spp. (Table 1). No fruits ever resulted from visits by small bees (body length ≤ 7 mm) in the family Halictidae (*Augochlorella* spp., *N* = 25 visits, and *Lasioglossum* spp., *N* = 8), the

non-native honey-bee (*Apis mellifera* *N* = 5 visits), and bees of the tribe Anthidiini (*N* = 1). Visits by flies (Diptera; *N* = 10) and butterflies (Lepidoptera; *N* = 1) also failed to result in any fruit set.

For *F. cylindraceus*, most of the visits observed were by the three cactus bees (Table 1). Among these, visits by *D. rinconis* were by far the most frequent. For *F. wislizeni*, 65 (1997) to 80% (1996) of visits were received from cactus bees. For *F. wislizeni*, in 1996 visits by *S. duplocincta* were the most abundant (64%), whereas in 1997 and 1998, visits were almost exactly evenly divided among the three cactus bees.

For *F. cylindraceus*, the mean number of seeds that resulted from a single pollinator visit (among those visits that resulted in a fruit), was 149 (range: 11–896). For *F. wislizeni*, the mean was 148 (range: 2–951).

Visit type did not have a significant effect on fruit set for *F. cylindraceus* (likelihood ratio = 1.180, df = 3, *P* = 0.7579, *N* = 180). The effect of bee species was not tested because there were so few visits other than *D. rinconis* visits to *F. cylindraceus* flowers (*D. rinconis*: 181 visits, *S. duplocincta*: 16, *A. opuntiae*: 6). In a nominal logistic model fit test of the effects of bee species and visit type on fruit set in *F. wislizeni* (pooled across years), bee species was significant and visit type was not (Table 2). Visits by *D. rinconis* to *F. wislizeni* resulted

Table 2. Effect of bee species (three cactus bees) and visit type on fruit set for *F. wislizeni* (*N* = 259 visits). Significant values are in bold type. Model R^2 = 0.0531

	df	Wald χ^2	<i>P</i>
Bee species	2	11.6465019	0.0030
Visit type	3	2.4596858	0.4826

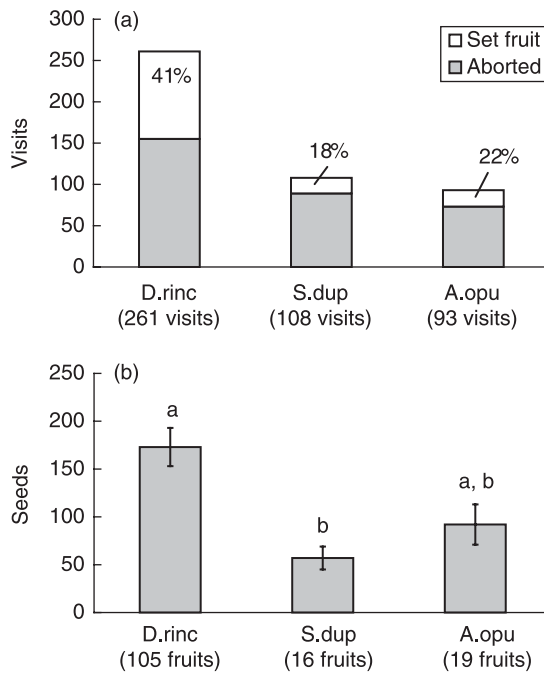


Fig. 1. Pollinator effectiveness, quality components, for the three cactus bees. Visits pooled across years and across *Ferocactus* species: (a) percentage fruit set; (b) mean seeds per fruit \pm SE. Means with different letters were significantly different in a post-hoc Tukey–Kramer HSD comparison. A.opu = *A. opuntiae*, D.rinc = *D. rinconis*, S.dup = *S. duplocincta*.

in a greater fruit set than visits by either *S. duplocincta* or *A. opuntiae* (Fig. 1a).

Visit type did not have a significant effect on seeds per fruit for *F. cylindraceus* ($\chi^2 = 1.3494$, df = 3, $P =$

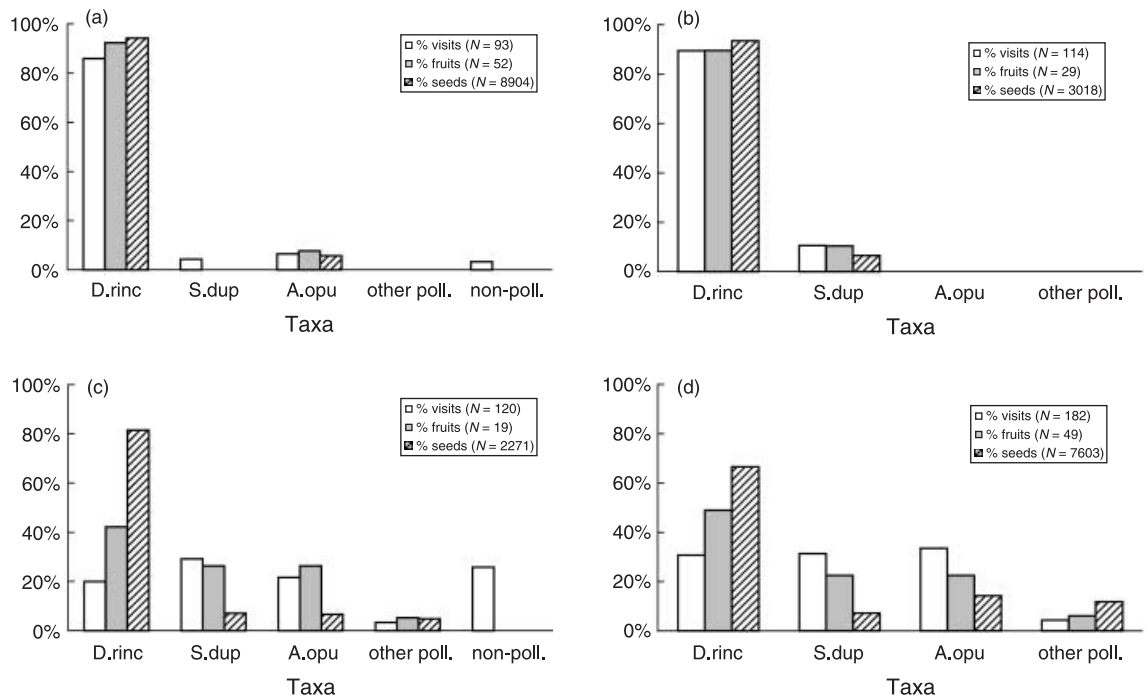


Fig. 2. Relative abundances and pollinator effectiveness of bee taxa visiting *Ferocactus* flowers. A.opu = *A. opuntiae*, D.rinc = *D. rinconis*, S.dup = *S. duplocincta*, other poll. = other pollinating taxa, non-poll. = non-pollinating taxa. In 1998 visits by small non-pollinators were not recorded; hence this category is not included: (a) 1996 & 1997 visits to *F. cylindraceus*; (c) 1996 & 1997 visits to *F. wislizeni*; (d) 1998 visits to *F. wislizeni*.

Table 3. Wilcoxon/Kruskal–Wallis tests for effects on seeds per fruit, *F. wislizeni*. Fruits are used as the unit of observation ($N = 60$). Significant values are in bold

	χ^2	df	P
Bee species	7.1262	2	0.0284
Visit type	3.6069	3	0.3072

0.7174, $N = 73$). In Wilcoxon/Kruskal–Wallis tests of the effects of bee species and visit type on seeds per fruit in *F. wislizeni* (pooled across years), bee species was again the only significant factor (Table 3). A post-hoc Tukey–Kramer HSD comparison showed that visits by *D. rinconis* resulted in significantly more seeds per fruit than visits by *S. duplocincta* (Fig. 1b). Nectar visits were the most abundant visit type for all three cactus bees, and thus resulted in the most total seeds (data not shown).

Visit abundance and per-visit pollinator quality can differ in the strength of their effect on total fecundity (percentage of all seeds produced by observed visits). Differences among the three cactus bees in visit abundance had a much greater effect on *F. cylindraceus* fecundity than did differences in per-visit effectiveness (Fig. 2a,b). In contrast, on *F. wislizeni*, visit abundances were almost exactly equal among the three cactus bees, but the greater per-visit effectiveness of *D. rinconis* visits, in terms of both fruit set and seeds per fruit, meant that *D. rinconis* visits accounted for most of the fecundity (Fig. 2c,d). Thus, with regard to visits by the three cactus bees pooled across years, although visits by *D. rinconis*

accounted for only 33% of all visits to *F. wislizeni*, they resulted in 79% of all seeds.

Overall, female bees visited flowers more often than male bees, for both *D. rinconis* and *S. duplocincta* (data not shown). Female to male ratios at flowers ranged from 2.5:1 to 3.5:1 for *D. rinconis*, and from 2.2:1 to 3:1 for *S. duplocincta*. There was considerable among-year variation in these proportions. On *F. cylindraceus*, in 1996–97 only male *S. duplocincta* were observed, whereas in 1998 only female *S. duplocincta* appeared. On *F. wislizeni*, female:male ratios for *D. rinconis* were 0.56:1 in 1997, but 14:1 in 1998. Also on *F. wislizeni*, female and male *S. duplocincta* visits were about equal in 1996 and 1997, but the female to male visit ratio was 4.5:1 in 1998.

Male and female bees did not differ in per-visit fruit set, for either *D. rinconis* ($\chi^2 = 0.086$, $df = 1$, $P = 0.7697$, $N = 261$ flowers) or *S. duplocincta* ($\chi^2 = 0.004$, $df = 1$, $P = 0.9473$, $N = 105$ flowers). Male and female bees also did not differ in per-visit seeds set per fruit, for either *D. rinconis* (Kruskal–Wallis test, $\chi^2 = 0.2701$, $df = 1$, $P = 0.6033$, $N = 105$ fruits) or *S. duplocincta* (Kruskal–Wallis test, $\chi^2 = 0.3888$, $df = 1$, $P = 0.5329$, $N = 16$ fruits). However, because female bees visited more than male bees, female visits were responsible for a higher proportion of total seeds produced (data not shown).

Discussion

This study provides a counter-example to the popular notion that plant-pollinator systems are mostly generalized. The visitor assemblages of both species of *Ferocactus* were dominated by three species of cactus-specialist bees (a functional group), and these bees were virtually the only pollinators of these plants.

Some cacti may have more diverse assemblages than those observed here. Mandujano, Montana & Eguiarte (1996) found that 89% of all visits recorded to *Opuntia rastrera* were by cactus-specialist bees. However, Johnson (1992) found that only 30% of all visits to *Echinomastus* were by cactus bees. Other pollination studies of cacti have not reported visit numbers broken down by taxa.

The introduced honey-bee (*Apis mellifera*), which is commonly found on *Prosopis*, *Cercidium* and *Carnegiea* flowering at the same time and near *F. cylindraceus* plants (M. E. McIntosh, unpublished observation), rarely visited *Ferocactus* flowers (Table 1). This is in agreement with other studies that found few honey-bees on cacti (Schmidt & Buchmann 1986; Osborn, Kevan & Lane 1988; McFarland, Kevan & Lane 1989). Also absent were the generalist bees *Bombus* (bumble-bees) and *Xylocopa* (carpenter bees), both common in the Sonoran desert in Arizona.

The cactus-specialist bees were even more dominant among the pollinating visitors than they were among visitors in general. Of visits that resulted in a mature fruit, 99% (*F. cylindraceus*) and 94% (*F. wislizeni*) were by cactus bees. Other visitors were either effective pol-

linators but rare (*Megachile* and *Halictus* spp.), or were relatively common but never pollinated the flowers (small halictids such as *Augochlorella* spp.; Table 1). However, although some types of visitors did not pollinate flowers with a single visit, it is quite possible that multiple visits by such visitors will actually lead to fruit set and seed production. Thus at times or in areas where the cactus bees observed in this study do not occur, the plants might still be able to reproduce.

A single visit to a *F. cylindraceus* flower resulted in a mean of 149 seeds; mean seeds per fruit for open-pollinated flowers was 575 (McIntosh 2002b). Thus, from one visit, *F. cylindraceus* flowers received roughly 26% of the pollen needed to set the average number of seeds in an open-pollinated fruit. For *F. wislizeni*, the mean number of seeds that resulted from a single was 148; mean seed set for open-pollinated flowers was 724. Thus, *F. wislizeni* flowers received roughly 20% of the pollen needed to match the seed set of open-pollinated flowers. Because visitation rates are relatively high (a visit usually occurred within 15 min of removing the cover), and the flowers are open for several days, it is probable that these flowers receive all the pollen they need to achieve an average seed set in the first day of opening. Data from a previous study demonstrated that these plants are not pollen-limited (McIntosh 2002b).

Previous work on the pollination biology of *Ferocactus* species is limited to two observational studies of visitors to *F. wislizeni* that do not report abundances or visitation rates (Grant & Grant 1979; Simpson & Neff 1987). These studies recorded species of *Lithurge*, *Diadasia*, *Megachile* and *Perdita echinocacti* as visitors to *F. wislizeni* (all but *Megachile* are cactus specialists). Other studies of the pollination of cacti with large, open-bowl flowers have not directly measured pollinator effectiveness (e.g. Mandujano *et al.* 1996).

Previous studies comparing the pollination effectiveness of specialist vs generalist bees on a single plant species have found no difference (Motten *et al.* 1981; Neff & Simpson 1990; Keys *et al.* 1995). It is likely that the cactus bees observed in this study were effective pollinators because they are relatively large and hairy, not because they are specialists. Likewise, the fact that most of the (generalist) halictids observed here were small and relatively hairless is probably what prevented them from being effective pollinators. If they had been small, relatively hairless cactus specialists, they would probably still be ineffective pollinators.

This study found that of the two factors contributing to the total realized fecundity of *Ferocactus* plants, the abundance (quantity) component was the most important. Nectar visits were more abundant than any other visit type, for all three cactus bees, suggesting that the cost of producing nectar might be offset by the gain in quantity of pollinator visits.

Because visitors must use different behaviours to collect pollen vs nectar in *Ferocactus* flowers, it was expected that pollen-collecting visits would be significantly

different in per-visit quality than nectar-collecting visits. This was not the case: there were no significant differences between pollen-collecting visits and nectar-collecting visits. Previous studies examining the benefits to the plant of nectar visits vs pollen visits have reached contrasting conclusions (e.g. Conner, Davis & Rush 1995; Gomez & Zamora 1999; Cane & Tepedino 2001). It is likely that effectiveness of visits is affected more by species-specific interaction characteristics (such as floral morphology) than by the type of reward collected.

These results are in accord with the recent finding that the structure of flower/flower–visitor interaction webs are often nested, with specialized organisms interacting primarily with a subset of their potential partners that are more generalized (Bascompte *et al.* 2003; Dupont, Hansen & Olesen 2003). In this case, specialized bees visit a generalized plant that hosts many visitors. However, these results also demonstrate the well-documented observation that not all visitors are pollinators – a fact that is overlooked by many studies of plant–‘pollinator’ (actually plant–visitor) interaction webs (Dicks, Corbet & Pywell 2002; Bascompte *et al.* 2003).

This study has several limitations. The single-pollinator visit method characterizes pollinator effects on only the female reproductive success of plants, and also does not address the conditionality of pollinator effectiveness (Thompson & Pellmyr 1992; Thomson & Thomson 1992). This method does, however, distinguish outcross from self pollen, because in these plants self pollen will result in almost no seeds. Also, because these plants have a very high rate of fruit set under natural conditions, if a single visit does not result in a fruit, it is likely because of deficiencies in the quantity or quality of pollen, not from postpollination effects such as resource limitation. These plants produce very large numbers of seeds under natural conditions, but they will also set a fruit with a relatively small number of seeds, hence the single-pollinator visit methods enables one to measure the quantitative effect of a visit (seed number), not just the qualitative effect (fruit set). Finally, this method provides a common basis for comparing diverse visitors, and because it is commonly used, it facilitates comparisons among studies.

I did not directly measure the abundance or visitation rates of different taxa, and visits were recorded only between 09:00 and 13:00 hours. This limited observation period probably sampled the vast majority of floral visitors, however (as was also found by Mandujano *et al.* 1996; Minckley *et al.* 1999). Only one population of each plant species was studied, and it is probable that the visitor assemblages and pollinator assemblages of these plants are geographically variable. A recent study of visitors to *F. wislizeni* flowers at a location partway between the two sites in this study found a markedly different taxonomic composition of the visitor fauna (dominated by small halictid bees; A. Eaton-Mordas, personal communication). Studies of floral

visitors to *Ferocactus* in other localities are needed to determine if the dominance of specialist cactus bees observed here is prevalent elsewhere.

The effects of different groups or types of visits on the postdispersal success of plant offspring, effects which can potentially swamp predispersal effects, were not measured (Gomez 2000; Herrera 2000). A holistic approach that evaluates the overall effect of visit type or visitor group on the lifetime reproductive success of the is obviously preferable to a reductionist examination of slight differences in fruit or seed set due to visitor identity or visit types (Zamora 2000).

Conclusions

The most striking result of this study is that despite their generalized morphology, the flowers of both species of barrel cacti are predominantly visited by, and almost exclusively pollinated by, a handful of pollen-specialist bees. The lesson for pollination biologists is that, just as apparently specialized flowers may be visited and pollinated by a more diverse assemblage than one would assume from their appearance (Fishbein & Venable 1996), apparently generalized flowers may be visited and pollinated by a much more restricted group than would be expected.

Acknowledgements

I thank E. A. Bernays, J. L. Bronstein, L. A. McDade and the McDade Laboratory Group for critical comments that greatly improved the manuscript. The Agricultural Experimental Station at the University of Arizona kindly granted me permission to do field work on the Santa Rita Experimental Range. The main source of funding for this research was a Graduate Research Fellowship from the National Science Foundation. Further support was provided by the Department of Ecology and Evolution at the University of Arizona, a fellowship from the Graduate College of the University of Arizona, the Flinn Foundation, and the University of Arizona Research Training Group in the Analysis of Biological Diversification.

References

- Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003) The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences USA* **100**, 9383–9387.
- Bosch, J., Retana, J. & Cerda, X. (1997) Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community. *Oecologia* **109**, 583–591.
- Cane, J.H. & Payne, J.A. (1993) Regional, annual and seasonal variation in pollinator guilds: intrinsic traits of bees (Hymenoptera: Apoidea) underlie their patterns of abundance at *Vaccinium ashei* (Ericaceae). *Annals of the Entomological Society of America* **86**, 577–588.
- Cane, J.H. & Tepedino, V.J. (2001) Causes and extent of declines among native North American invertebrate

- pollinators. *Detection, Evidence, and Consequences. Conservation Ecology* **5**, 1. URL: <http://www.consecol.org/vol5/iss1/art1>.
- Conner, J.K., Davis, R. & Rush, S. (1995) The effect of wild radish floral morphology on pollination efficiency by four taxa of pollinators. *Oecologia* **104**, 234–245.
- Cota, J.H. & Wallace, R.S. (1997) Chloroplast DNA evidence for divergence in *Ferocactus* and its relationships to North American columnar cacti (Cactaceae: Cactoideae). *Systematic Botany* **22**, 529–542.
- Dicks, L.V., Corbet, S.A. & Pywell, R.F. (2002) Compartmentalization in plant–insect flower visitor webs. *Journal of Animal Ecology* **71**, 32–43.
- Dupont, Y.L., Hansen, D.M. & Olesen, J.M. (2003) Structure of a plant–flower–visitor network in the high-altitude sub-alpine desert of Tenerife, Canary Islands. *Ecography* **26**, 301–310.
- Fishbein, M. & Venable, D.L. (1996) Diversity and temporal change in the effective pollinators of *Asclepias tuberosa*. *Ecology* **77**, 1061–1073.
- Gomez, J.M. (2000) Effectiveness of ants as pollinators of *Lobularia maritima*: effects on main sequential fitness components of the host plant. *Oecologia* **122**, 90–97.
- Gomez, J.M. & Zamora, R. (1999) Generalization vs. specialization in the pollination system of *Hormathophylla spinosa* (Cruciferae). *Ecology* **80**, 796–805.
- Grant, V. & Grant, K.A. (1979) Pollination of *Echinocereus fasciculatus* and *Ferocactus wislizenii*. *Plant Systematics and Evolution* **132**, 85–90.
- Harder, L.D. & Barclay, R.M.R. (1994) The functional significance of poricidal anthers and buzz pollination: controlled pollen removal from *Dodecatheon*. *Functional Ecology* **8**, 509–517.
- Herrera, C.M. (1987) Components of pollinator ‘quality’: comparative analysis of a diverse insect assemblage. *Oikos* **50**, 79–90.
- Herrera, C.M. (1988) Variation in mutualisms: the spatio-temporal mosaic of a pollinator assemblage. *Biological Journal of the Linnean Society* **35**, 95–125.
- Herrera, C.M. (1989) Pollinator abundance, morphology, and flower visitation rate: analysis of the ‘quantity’ component in a plant–pollinator system. *Oecologia* **80**, 241–248.
- Herrera, C.M. (2000) Flower-to-seedling consequences of different pollination regimes in an insect-pollinated shrub. *Ecology* **81**, 15–29.
- Johnson, R.A. (1992) Pollination and reproductive ecology of *Acuna cactus Echinomastus erectocentrus* var *acumensis* Cactaceae. *International Journal of Plant Sciences* **153**, 400–408.
- Johnson, S.D. & Steiner, K.E. (2000) Generalization versus specialization in plant pollination systems. *Trends in Ecology and Evolution* **15**, 140–143.
- Keys, R.N., Buchmann, S.L. & Smith, S.E. (1995) Pollination effectiveness and pollination efficiency of insects on *Prosopis velutina* in southeastern Arizona. *Journal of Applied Ecology* **32**, 519–527.
- Krombein, K.V., Hurd, P.D. Jr, Smith, D.R. & Burks, B.D. (1979) *Catalog of Hymenoptera in America North of Mexico*. Smithsonian Institution Press, Washington DC.
- Mandujano, M.D.C., Montana, C. & Eguiarte, L.E. (1996) Reproductive ecology and inbreeding depression in *Opuntia rastrera* (Cactaceae) in the Chihuahuan desert: why are sexually derived recruitments so rare? *American Journal of Botany* **83**, 63–70.
- McFarland, J.D., Kevan, P.G. & Lane, M.A. (1989) Pollination biology of *Opuntia imbricata* (Cactaceae) in southern Colorado. *Canadian Journal of Botany* **67**, 24–28.
- McIntosh, M.E. (2002a) Flowering phenology and reproductive output in two sister species of *Ferocactus* (Cactaceae). *Plant Ecology* **159**, 1–13.
- McIntosh, M.E. (2002b) Plant size, breeding system, and limits to reproductive success in two sister species of *Ferocactus* (Cactaceae). *Plant Ecology* **162**, 273–288.
- Michener, C.D. (2000) *The Bees of the World*. Johns Hopkins University Press, Baltimore, MD.
- Minckley, R.L., Cane, J.H., Kervin, L. & Roulston, T.H. (1999) Spatial predictability and resource specialization of bees (Hymenoptera: Apoidea) at a superabundant, widespread resource. *Biological Journal of the Linnean Society* **67**, 119–147.
- Motten, A.F., Campbell, D.R. & Alexander, D.E. (1981) Pollination effectiveness of specialist and generalist visitors to a North Carolina U.S.A. population of *Claytonia virginica*. *Ecology* **62**, 1278–1287.
- Neff, J.L. & Simpson, B.B. (1990) The roles of phenology and reward structure in the pollination biology of wild sunflower (*Helianthus annuus* L., Asteraceae). *Israel Journal of Botany* **39**, 197–216.
- Neff, J.L. & Simpson, B.B. (1992) Partial bivoltinism in a ground-nesting bee: the biology of *Diadasis rinconis* in Texas (Hymenoptera: Anthophoridae). *Journal of the Kansas Entomological Society* **65**, 377–392.
- Ollerton, J. (1996) Reconciling ecological processes with phylogenetic patterns: the apparent paradox of plant–pollinator systems. *Journal of Ecology* **84**, 767–769.
- Ordway, E. (1987) The life history of *Diadasis rinconis* Cockerell (Hymenoptera: Anthophoridae). *Journal of the Kansas Entomological Society* **60**, 15–24.
- Osborn, M.M., Kevan, P.G. & Lane, M.A. (1988) Pollination biology of *Opuntia polyacantha* Haw. & *Opuntia phaeacantha* Engelm. (Cactaceae) in Southern Colorado. *Plant Systematics and Evolution* **159**, 85–94.
- Pellmyr, O. & Thompson, J.N. (1996) Sources of variation in pollinator contribution within a guild: the effects of plant and pollinator factors. *Oecologia* **107**, 595–604.
- SAS Institute (1989–2002) *JMP 5.1*. SAS Institute, Cary, NC.
- Schmidt, J.O. & Buchmann, S.L. (1986) Floral biology of the Saguaro, *Cereus giganteus* I. Pollen harvest by *Apis mellifera*. *Oecologia* **69**, 491–498.
- Simpson, B.B. & Neff, J.L. (1987) Pollination ecology in the arid southwest. *Aliso* **11**, 417–440.
- Sipes, S.D. & Wolf, P.G. (2001) Phylogenetic relationships within *Diadasis*, a group of specialist bees. *Molecular Phylogenetics and Evolution* **19**, 144–156.
- Strickler, K. (1979) Specialization and foraging efficiency of solitary bees. *Ecology* **60**, 998–1009.
- Thompson, J.N. & Pellmyr, O. (1992) Mutualism with pollinating seed parasites amid co-pollinators – constraints on specialization. *Ecology* **73**, 1780–1791.
- Thomson, J.D. & Thomson, B.A. (1992) Pollen presentation and viability schedules in animal-pollinated plants: consequences for reproductive success. *Ecology and Evolution of Plant Reproduction* (ed. R. Wyatt), pp. 1–24. Chapman & Hall, New York.
- Wcislo, W.T. & Cane, J.H. (1996) Floral resource utilization by solitary bees (Hymenoptera: Apoidea) and exploitation of their stored foods by natural enemies. *Annual Review of Entomology* **41**, 195–214.
- Wilson, P. & Thomson, J.D. (1996) How do flowers diverge? Floral biology. *Studies on Floral Evolution in Animal-pollinated Plants* (ed. S.C.H. Barrett), pp. 88–111. Chapman & Hall, New York.
- Zamora, R. (2000) Functional equivalence in plant–animal interactions: ecological and evolutionary consequences. *Oikos* **88**, 442–447.
- Zavortink, T.J. (1975) Host plants, behavior, and distribution of the eucerine bees *Idiomelissodes duplocincta* (Cockerell) and *Syntrichalonia exquisita* (Cresson) (Hymenoptera: Anthophoridae). *Pan-Pacific Entomologist* **51**, 236–242.

Received 16 December 2004; revised 6 February 2005; accepted 17 February 2005