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The evolution of obligate pollination mutualisms: senita cactus and senita moth

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Abstract We report a new obligate pollination mutualism involving the senita cactus, *Lophocereus schottii* (Cactaceae, Pachycepherae), and the senita moth, *Upiga virescens* (Pyralidae, Glaphyriinae) in the Sonoran Desert and discuss the evolution of specialized pollination mutualisms. *L. schottii* is a night-blooming, self-incompatible columnar cactus. Beginning at sunset, its flowers are visited by *U. virescens* females, which collect pollen on specialized abdominal scales, actively deposit pollen on flower stigmas, and oviposit a single egg on a flower petal. Larvae spend 6 days eating ovules before exiting the fruit and pupating in a cactus branch. Hand-pollination and pollinator exclusion experiments at our study site near Bahia Kino, Sonora, Mexico, revealed that fruit set in *L. schottii* is likely to be resource limited. About 50% of hand-outcrossed and open-pollinated senita flowers abort by day 6 after flower opening. Results of exclusion experiments indicated that senita moths accounted for 75% of open-pollinated fruit set in 1995 with two species of halictid bees accounting for the remaining fruit set. In 1996, flowers usually closed before sunrise, and senita moths accounted for at least 90% of open-pollinated fruit set. The net outcome of the senita/senita moth interaction is mutualistic, with senita larvae destroying about 30% of the seeds resulting from pollination by senita moths. Comparison of the senita system with the yucca/yucca moth mutualism reveals many similarities, including reduced nectar production, active pollination, and limited seed destruction. The independent evolution of many of the same features in the two systems suggests that a common pathway exists for the evolution of these highly specialized pollination mutualisms. Nocturnal flower opening, self-incompatible breeding systems, and resource-limited fruit production appear to be important during this evolution.

Key words Pollination · Sonoran Desert · *Lophocereus schottii* · *Upiga virescens* · Yucca/yucca moths

Introduction

Although pollination by animals is common in angiosperm plants, obligate pollination mutualisms, especially those involving active pollination, are rare (Waser et al. 1996; Pellmyr 1997). Classic examples of these kinds of mutualisms include yuccas (*Yucca*) and yucca moths (*Tegeticula*, *Parategeticula*) (Riley 1892; Aker and Udovic 1981; Pellmyr et al. 1996), and figs (*Ficus*) and fig wasps (Agaonidae) (Janzen 1979; Wiebes 1979; Addicott et al. 1990). In both of these mutualisms, females actively pollinate flowers by deliberately collecting pollen and depositing it on or in receptive stigmas. Females oviposit eggs into ovaries, and their larvae eat a portion of the seed crop. These insects thus are pollinators and seed predators and simultaneously interact with their host plants as mutualists and antagonists. In addition to a net positive effect on seed set, conditions favoring the evolution of such specialized pollination mutualisms are thought to include a close physical relationship between large, long-lived plants and pollinators whose life cycles are synchronized with flowering phenology (Addicott et al. 1990; Bronstein 1992; Pellmyr and Huth 1994; Thompson 1994; Waser et al. 1996). Although co-pollinators are absent in the fig and yucca mutualisms, Pellmyr et al. (1996) predicted that active pollination can evolve in the presence of co-pollinators when specialized pollinator/seed predators provide higher-quality pollination than generalists.

Given the rarity of obligate pollination mutualisms, it has been difficult to test these predictions. Only in the case of the yucca/yucca moth system have phylogenetic studies been conducted that illuminate the evolutionary steps producing such a specialized interaction (Pellmyr et al. 1996). These studies reveal that several of the life-history traits found in yucca moths are widespread in the

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Prodoxidae. Only active pollination and modified mouthparts are unique to yucca moths. In his discussion of the evolution of active pollination, Pellmyr (1997) suggested that active pollination may be rare in nature because it requires certain preadaptations, including local host specificity and limited larval seed destruction, that transform an antagonistic interaction into a mutualistic one.

Here we report a new obligate pollination mutualism involving the Sonoran Desert columnar cactus *Lophocereus schottii* (Cactaceae, Pachycereae) (senita), and its moth pollinator, *Upiga virescens* (Pyralidae, Glaphyriinae) (senita moth). We describe the basic features of this interaction and compare them with those of the yucca/yucca moth system. Such a comparison allows us to assess how specialized pollination mutualisms evolve by addressing the following questions. (1) How general is the evolutionary pathway that produced the specialized yucca/yucca moth interaction? (2) How many similarities and differences with the yucca system occur in another independently evolved moth/plant mutualism? (3) What factors seem to be most important for the evolution of these mutualisms? Our comparison of the yucca and senita systems indicates that they possess many similarities, which suggests that these highly specialized pollination mutualisms are the products of a common evolutionary pathway.

Materials and methods

This study was conducted in April and May 1995 and April through early July 1996 near Bahia Kino, Sonora, Mexico. Our study site is located in the Central Coastal region of the Sonoran Desert (Shreve and Wiggins 1964) and has been described elsewhere (Fleming et al. 1996). In 1995 and 1996 we worked on a 20-ha plot in which we tagged and mapped 155 flowering adults (7.8 adults/ha); in 1996 we also worked at a second site 2.5 km north of site 1 which contained the same density of adult senitas.

The study organisms

L. schottii is a common member of the Sonoran Desert vegetation in mainland Mexico and Baja California. This multi-branched columnar cactus attains a height of 2–4 m and lives for up to 75 years (Shreve 1935). The apices of its branches bear a thick layer of 5- to 10-cm-long spines which cover a majority of its reproductive areoles (spine-bearing pads that produce flower buds). It has an extended flowering season that lasts from late March or early April to August (Shreve and Wiggins 1964). At our study site, plants produce up to 400 small flowers (mass = 1.6 ± 0.1 g, $n = 10$) per night and over 3,000 flowers per season (J.N. Holland and T.H. Fleming, submitted). Flowers produce small amounts of pollen and either small amounts of nectar ($\leq 1 \mu\text{l}$) or none at all. In 1996, 10 of 20 plants whose flowers were covered with bridal veil netting just before opening and sampled at sunrise with a 2- μl capillary tube contained no nectar ($n = 2$ –5 flowers/plant). Mature fruits are small berries (mass = 4.5 ± 0.3 g, $n = 7$) containing 182 ± 11 ($n = 30$) mature seeds (J.N. Holland and T.H. Fleming, submitted). Senita reproduces both sexually and vegetatively (Parker and Hamrick 1992).

Prior to our studies, little was known about the life history of the senita moth, *U. virescens*. Munroe (1972) reported that its larvae occur in fruits of *L. schottii*. It has been collected at various

locations in the Sonoran Desert of mainland Mexico, Baja California, and southwestern Arizona. Adult wing length measures 8–9 mm (Fig. 1), and adults weigh about 25 mg. We conducted a detailed study of adult moth behavior and the life-history of *U. virescens* in 1996 (J.N. Holland and T.H. Fleming, submitted).

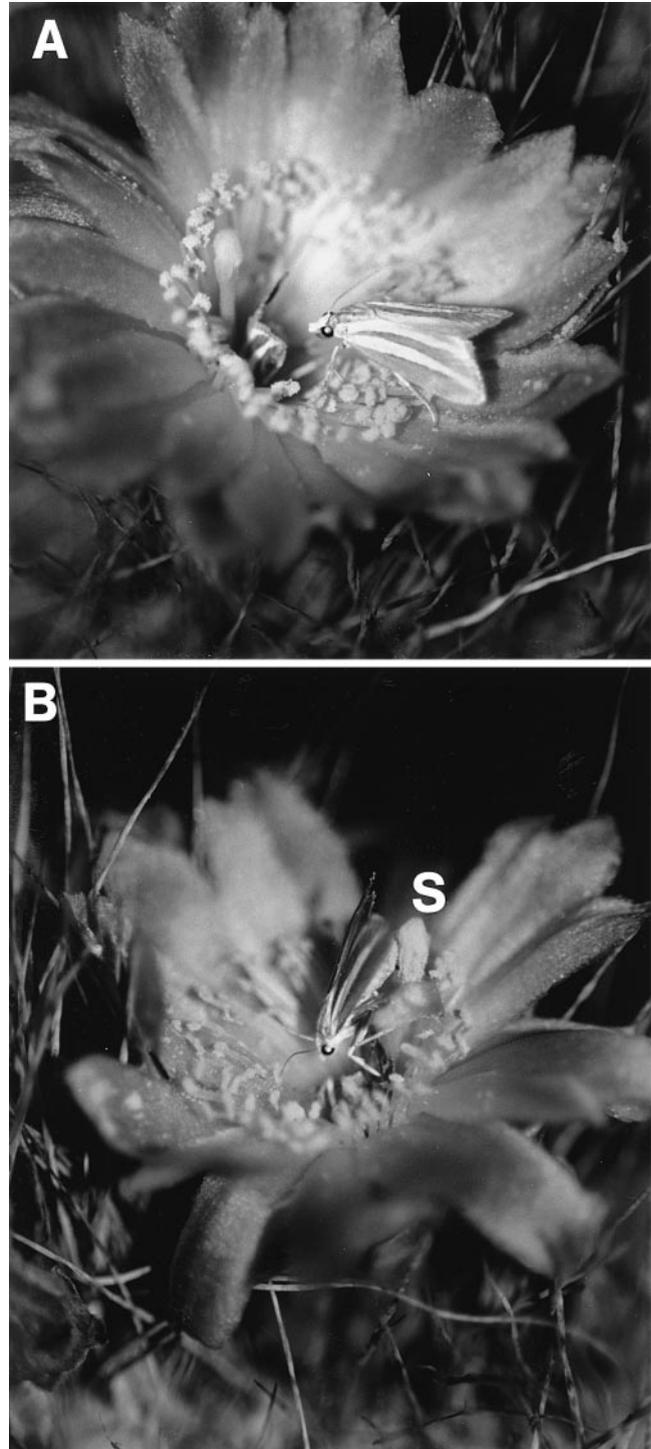


Fig. 1 A Two adult senita moths (*Upiga virescens*) on a senita cactus (*Lophocereus schottii*) flower. The moth on the left is nectaring; the moth on the right has just collected a load of pollen on its abdomen. B An adult female depositing pollen on a senita stigma (S)

Here we will summarize our major findings for comparison with the yucca/yucca moth system.

Methods

We conducted hand-pollination experiments in 1995 to determine the compatibility system of senita and whether fruit set is pollen limited. To test for self-compatibility, we dusted the stigma of a total of 27 newly opened flowers on eight plants with fresh pollen from another flower on the same plant. Flowers were bagged with bridal veil netting (mesh = 1 mm) before and after pollination. To determine fruit set in the absence of pollen limitation, we dusted the stigmas of another group of 28 flowers on a total of six plants with fresh pollen from one flower of another plant. These flowers were not covered with netting. Fruit initiation begins soon after flower closing in *L. schottii*, and fruit abortion owing to lack of pollination or resource limitation occurs within 6 days of flower closing. We scored flower fate (aborted or not) 1 week after hand pollination.

We conducted pollinator exclusion experiments in 1995 and 1996 to determine the relative contribution of nocturnal and diurnal flower visitors to fruit set in senita. Three treatments were applied to the same ten plants in both years. Treatments included open-pollinated control flowers which were not covered with bridal veil netting, nocturnally pollinated flowers which were available to pollinators at night before being covered with netting before sunrise, and diurnally pollinated flowers which were covered with netting at night and uncovered before sunrise. Sample sizes were 94 flowers per treatment in 1995 and 265–269 flowers per treatment in 1996. Flower fate (aborted or not) was scored 1 week after flowers closed.

To identify nocturnal and diurnal pollinators, we censused many flowers between 1930 and 0100 hours MST in both years and after sunrise in 1995. To determine whether both males and females of *U. virescens* are pollinators, we used small plastic vials to capture a total of 119 moths on senita plants between 2000 and 2130 hours MST on two nights in 1996. Moths were preserved in alcohol and examined for pollen in the laboratory.

In May 1996 we tagged a total of 2,290 flowers on 60 plants the morning they closed and determined whether they aborted, abscised owing to larval attack, or became mature fruits. At 3-day intervals, we examined a random subset of 25–71 of these flowers or fruit for moth larvae. Fruit containing moth larvae were scored as “dead” because all fruit attacked by larvae abscise. Fruit that lacked a larva were scored as “alive” and were assumed to survive to maturity because, except for resource-limited abortion that occurs between days 1–6 after flower closing, very few unattacked fruit abscised. From flower/fruit survivorship data we calculated the ratio of benefit to cost for the senita/senita moth interaction as percent fruit set contributed by senita moths divided by percent fruit destroyed by senita moth larvae. Specifically, we estimated the benefit by multiplying percent fruit survival on day 6 by percent of control fruit set contributed by senita moths. We estimated the cost as the difference between percent fruit survival on day 6 and day 15, the period when fruit abscission owing to attack by senita larvae occurs.

Results

Results of the hand pollination experiments indicated that senita flowers are self-incompatible and that fruit set is likely to be resource limited. None of the selfed flowers set fruit (Table 1). When flowers were provided with abundant outcross pollen, only 46% initiated fruit development. This value did not differ from percent fruit set in open-pollinated flowers in the 1995 pollinator exclusion experiment ($\chi^2 = 0.033$, $df = 1$, $P = 0.86$, Table 1). Results of similar outcross experiments at Organ Pipe Cactus National Monument, Pima County, Arizona, in 1997 also support our conclusion that fruit set is likely to be resource-limited in senita (J.N. Holland and T.H. Fleming, unpublished data).

Our flower censuses and results of the exclusion experiments indicated that pollination by senita moths accounted for most fruit set in both years. Senita moths were the only nocturnal pollinators of senita flowers. In 1995, when morning temperatures were unusually low in April and May and flowers stayed open until about 0900 hours MST, pollination by senita moths accounted for 75% of control fruit set (Table 1). Two species of bees, *Augochlorella* sp. and *Agapostemon melliventer* (Halictidae), visited flowers beginning at sunrise and accounted for the remaining 25% fruit set. These bees are common visitors to flowers of other columnar cacti at our study site (T.H. Fleming and J.N. Holland, personal observation). Similar experiments in 1996, which was a warmer year in which flowers usually closed before sunrise and excluded diurnal pollinators, indicated that senita moths accounted for at least 90% of control fruit set (Table 1). A three-way log-linear analysis involving year, treatment, and flower fate (i.e., fruit set or not) indicated that the three-way interaction was significant ($G = 12.72$, $df = 2$, $P < 0.005$) and that years differed holding treatment and fate constant ($G = 14.93$, $df = 5$, $0.025 < P < 0.01$). From these experiments, we conclude that nocturnal senita moths are temporally more reliable pollinators than diurnal co-pollinators because of annual differences in time of flower closing.

All phases of the life-history of the senita moth *U. virescens* are associated with the senita cactus (J.N. Holland and T.H. Fleming, submitted). During the day,

Table 1 Results of the hand pollination and pollinator exclusion experiments on senita cactus at Bahia Kino, Sonora, Mexico

Treatment	Number of plants	Total number of flowers	Percent fruit initiating development
Hand pollination			
Self pollination	8	27	0.0
Outcross	6	28	46.4
Pollinator exclusion			
Open-pollinated 1995	10	94	46.8
Nocturnal pollination 1995	10	94	35.1
Diurnal pollination 1995	10	94	23.4
Open-pollinated 1996	10	268	44.0
Nocturnal pollination 1996	10	269	39.8
Diurnal pollination 1996	10	265	7.9

adult moths rest cryptically on the long spines that cover the upper parts of senita branches. As soon as flowers open at sunset, female senita moths interact with them in four ways. (1) They actively collect pollen by rubbing their abdomens, whose terminal segments are covered with a brush of relatively long, thin scales (Fig. 2A), across dehiscent anthers to collect a mass of pollen grains (Fig. 1A). (2) They actively deposit pollen on the erect stigma of a flower by assuming a head-down position and rubbing their pollen-covered abdomen over its surface for 18–20 s (Fig. 1B). (3) They oviposit an egg on the tip of a flower petal. (4) They sometimes crawl deeply into the corolla where they presumably drink nectar. Male moths are present on senita cacti at night but are not involved in pollination. None of 50 males, whose abdomens lack a pollen brush (Fig. 2C), carried pollen at the time of their capture; 64 of 69 females (92.7%) captured at the same time were carrying pollen.

After eggs hatch, moth larvae crawl to the bottom of closed corollas, chew through the ovary wall, and begin to eat developing seeds. Mortality is high during this stage of the moth life cycle; about 20% of the larvae survive to become seed predators (J.N. Holland and T.H. Fleming, submitted). Single larvae are present in developing fruits between days 6 and 12 after flower closing (Fig. 3). Before destroying the entire seed crop, they chew through the base of the fruit and enter the cactus branch where they pupate. Fruit that contained a moth larva abscised so that seed mortality in these fruits is 100%. Low larval survival reduces the cost of this interaction to the plant and makes it strongly mutualistic.

In 1996, 36% of flowers set fruit from senita moth pollination, and about 24% of senita flowers matured into ripe fruits (Fig. 3). Fruit loss occurred primarily from two sources: (1) 55–60% of all flowers aborted within 6 days of closing and (2) 16–21% abscised during fruit maturation, owing primarily to damage from senita larvae. Larvae of a second species of pyralid moth, *Cactobrosis fernandialis*, which also feed on fruits and seedlings of saguaro cactus, *Carnegie gigantea* (Steenbergh and Lowe 1977), were present in a few fruit between days 13–19 (Fig. 3). The ratio of benefit to cost to the senita cactus from its interaction with *U. virescens* is about 3.4 (i.e., 35.6% fruit set from senita moth pollination/10.5% fruit destruction by senita larvae; Fig. 3). Senita larvae destroyed about 30% of the fruits (and seeds) resulting from pollination by senita moths.

Discussion

The senita cactus/senita moth mutualism represents the third known evolved obligate pollination mutualism involving active pollination. Two examples of such mutualisms involve moths and occur in plants living in arid regions of North America. Below we review evolutionary trends within the lineages containing yuccas and the senita cactus and their pollinators before dis-

cussing the possible evolutionary pathways that have produced these mutualisms.

Evolutionary trends in the reproductive biology of Agavaceae have been summarized by Pellmyr et al. (1996). Fruit production is resource limited in basal members of this family as well as in the highly derived *Yucca*, which is paraphyletic (Bogler et al. 1995). Nocturnally opening flowers and ample nectar production are common in basal members; nocturnal flowering is retained but nectar production has been lost in *Yucca*. Basal members are pollinated by a broad spectrum of generalized pollinators; specialized pollination in *Yucca* is derived.

The pollinators of *Yucca* are also highly derived (Pellmyr et al. 1996). Local host specificity, an important precursor for the evolution of pollination specialization, is common in moths of the Prodoxidae. Oviposition into flowers has evolved two to three times in this family, and limited larval seed destruction is widespread. Passive pollination has evolved twice within moths of the genus *Greya*, which is the sister genus to yucca moths, but active pollination has evolved only once in the ancestor of yucca moths *Tegeticula* and *Parategeticula*. Only active pollination and mouthparts specialized for collecting pollen are unique to yucca moths.

L. schottii is a derived member of subtribe Pachycerinae, family Cactaceae. Its closest relative apparently is *Pachycereus marginatus*, a hummingbird-pollinated cactus of central Mexico (Gibson and Horak 1978; Cota and Wallace, in press). Basal members of this subtribe bear large flowers that usually open nocturnally, produce large amounts of nectar and pollen, and are pollinated by bats in relatively short blooming seasons (Fleming et al. 1996, Valiente-Banuet et al. 1996). Resource-limited fruit set occurs in the saguaro cactus (*C. gigantea*), but fruit set is pollen limited in females of the trioecious cactus, *Pachycereus pringlei* (Fleming et al. 1996). In addition to reduced flower size, senita differs reproductively from basal members of its subtribe in two other features (Gibson and Horak 1978): (1) its reproductive areoles produce two or more buds, rather than a single bud, per flowering season, which results in high flower production, and (2) its pollen grains bear the largest spinules in the subtribe, probably facilitating their collection by senita moths (Fig. 2D).

Evolutionary steps leading to active pollination in the senita moth are currently unknown. If its evolution was similar to that of *Tegeticula* and *Parategeticula* moths (Pellmyr et al. 1996), we predict that relatives of the senita moth will oviposit eggs on or near the ovaries of other Cactaceae and/or will passively pollinate cactus flowers while nectaring. Behavioral and phylogenetic studies are needed to clarify the evolution of active pollination in the senita moth.

A summary of the major features of the yucca/yucca moth and senita/senita moth systems reveals a number of similarities and differences (Table 2). Major similarities include: (1) both mutualisms involve resource-limited fruit set with water likely being the limiting resource

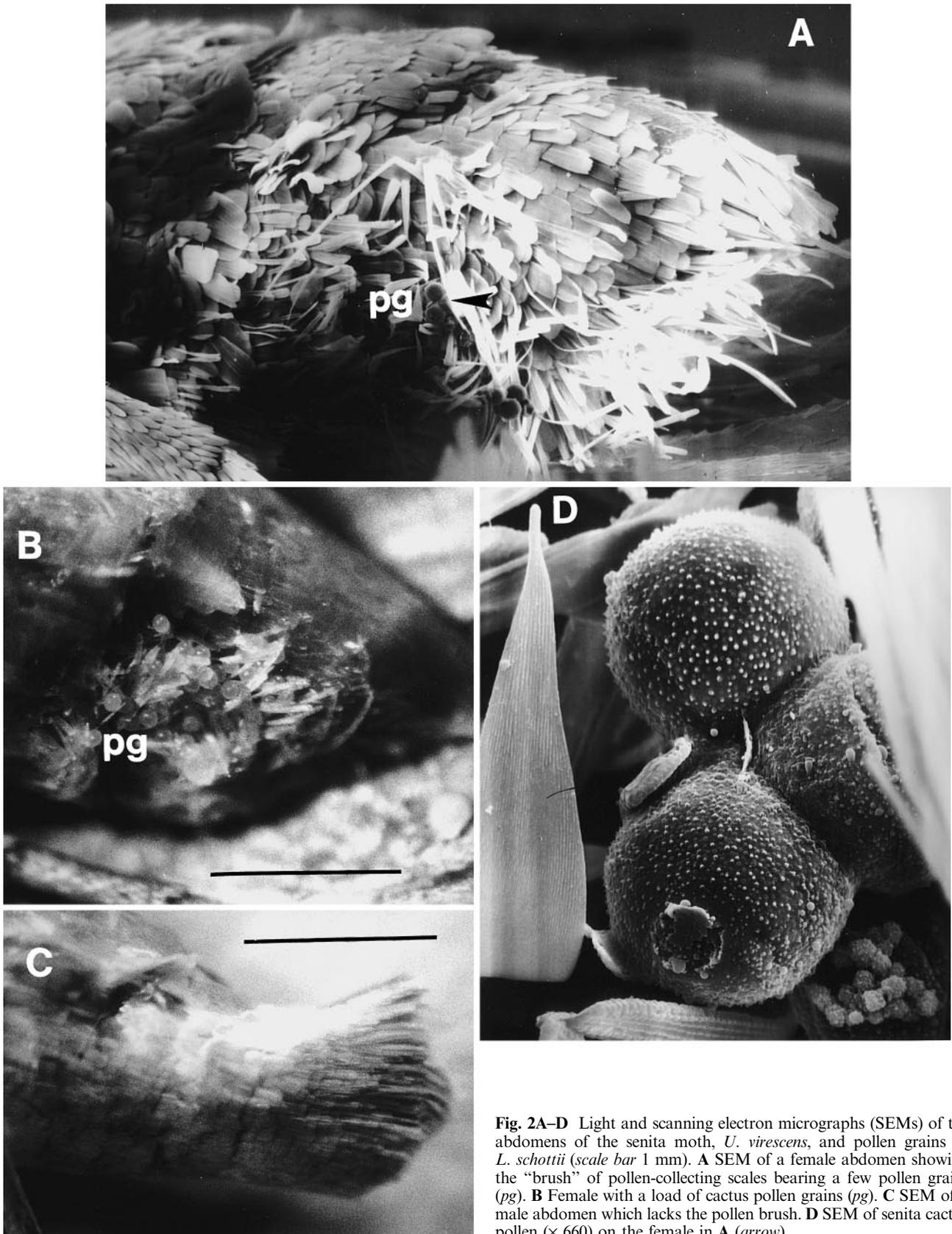


Fig. 2A–D Light and scanning electron micrographs (SEMs) of the abdomens of the senita moth, *U. virescens*, and pollen grains of *L. schottii* (scale bar 1 mm). **A** SEM of a female abdomen showing the “brush” of pollen-collecting scales bearing a few pollen grains (pg). **B** Female with a load of cactus pollen grains (pg). **C** SEM of a male abdomen which lacks the pollen brush. **D** SEM of senita cactus pollen ($\times 660$) on the female in **A** (arrow)

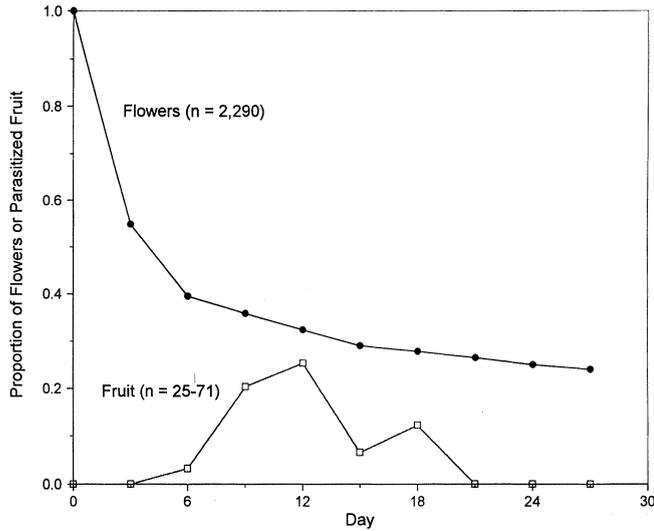


Fig 3 Survivorship curve for flowers/fruit of the senita cactus in May 1996. A total of 2,290 flowers on 60 plants was tagged. Flower/fruit loss prior to day 6 reflects resource-limited abortion. Fruit loss from day 6 on occurs mainly as a result of abscission caused by larvae of the senita moth (days 6–12) or another pyralid moth, *Cactobrosia fernandialis* (days 13–19). The time lines for both curves are the same and reflect days since flower closing

(Nobel 1988); (2) flowers are self-incompatible and produce little or no nectar; (3) female moths are active pollinators and collect pollen with specialized structures; (4) co-pollinators are temporally unreliable (senita) or absent (yucca), and (5) larvae destroy 20–30% of the seed crop, yielding benefit:cost ratios of 2–5. Major differences between these systems include: (1) the senita cactus has an extended flowering season; (2) the senita moth has several generations per flowering season; (3) senita fruit contain a single moth larva; (4) seed destruction per fruit is 100% in senita, and (5) senita larvae pupate in senita branches rather than in soil.

The large number of similarities in these independently derived mutualisms suggests that they have evolved in response to similar selection pressures, including selection for reduced nectar production in the plants and specialized pollen-collecting structures and active pollination behavior in the moths. As predicted by theory (Addicott et al. 1990; Thompson 1994; Waser et al. 1996), both systems feature pollinators whose life cycles are intimately associated with long-lived plants with seasonal flowering cycles. We propose that three of their common features—nocturnal flower opening, self-incompatibility, and resource-limited fruit set—have

Table 2 Comparison of yucca and senita pollination mutualisms. Based on Shreve and Wiggins (1964), Addicott (1986), Powell (1992), Dodd and Linhart (1994), Bogler et al. (1995), Pellmyr et al. (1996), O. Pellmyr (personal communication), and J.N. Holland and T.H. Fleming (submitted)

Trait	Yucca/yucca moth	Senita/senita moth
Plants		
Number of species	ca. 40	2
Geographic range	Widespread in arid parts of North America	Restricted to Sonoran Desert
Vegetative reproduction?	Yes	Yes
Flowering season	3–4 days to 6 weeks	20 weeks
Flowers/plant/season	Several hundred to several thousand	Several thousand
Flower opening	Nocturnal	Nocturnal
Flower lifespan	> 1 day	< 12 h
Breeding system	Self-incompatible	Self-incompatible
Nectar production	None or little	None or little
Fruit production	Resource-limited (ca. 10% fruit set)	Resource-limited (ca. 45% fruit set)
Fruit type	Dry or fleshy capsule	Berry
Moths		
Number of species	≥3 <i>Tegeticula</i> , 1 <i>Parategeticula</i>	1
Do adults feed?	No?	Yes
Where do adults mate?	In flowers	On cactus spines
Active pollination?	Yes	Yes
Specialized pollen-collecting structures?	Yes	Yes
Co-pollinators?	No	Present but variable in effect by year
Oviposition site	In flower locule, scape, or pedicel	On flower petal
Number of eggs per flower	Several	1 (rarely 2–3)
Number of larvae per fruit	≤ 6	1
Percent seed destruction per fruit	Variable: 3–30%	100% (attacked fruits abscise)
Ratio of percent fruits or seeds produced to percent fruits or seeds destroyed	2.3–4.0	ca. 3.4
Generations per year	1	4–5
Pupation site	In soil	In cactus branch

been important during the evolution of these obligate mutualisms.

Nocturnal flower opening is important for the evolution of these mutualisms because it limits the number of potential flower visitors to moths. Thompson and Pellmyr (1992) have argued that selection does not favor a specialized mutualism between *Greya* moths, which are diurnal, and *Lithophragma* plants because of the presence of abundant and effective co-pollinators, including bombyliid flies and a variety of bees. Co-pollinators are completely absent in the yucca system but are present in the senita system. Although our pollinator exclusion experiments indicate that halictid bees are effective pollinators of senita flowers, temperature-dependent flower closing in senita reduces their overall contribution to fruit set, probably both within and between years (cf. 1995 and 1996) compared to that of the senita moth (J.N. Holland and T.H. Fleming, unpublished data). Because it is nocturnal, the senita moth is a temporally more reliable pollinator than diurnal halictid bees, and hence selection may continue to favor plant traits, including flower closing at or before sunrise and reduced nectar production, that promote pollination by this species.

Self-incompatibility is another common feature of the yucca and senita systems that favors the evolution of specialized pollination behavior. This breeding system selects for pollinators that visit flowers on different conspecific plants. Because they oviposit an egg or eggs on or in flowers, female yucca moths and senita moths are under strong selection to be effective outcrossers. Self-incompatibility selects for effective pollen collection on one flower and effective pollen deposition on the stigma of another conspecific individual in ovipositing pollinators. It is unlikely that active pollination will evolve in plants with self-compatible breeding systems.

Resource-limited fruit set and reduced nectar production also characterize the yucca and senita systems. Pellmyr et al. (1996, p 843) state that "Cessation of nectar production may have been adaptive for fruit production, and water reallocation within yuccas may have been the ultimate cause for evolution of pollination specialization in these plants." A similar argument may apply to senita cacti, which Parker (1988) suggests are more water limited than saguaro and organ pipe cacti in the Sonoran Desert. Selection for reduced nectar production, especially when unfertilized ovules rather than nectar or pollen is the primary reward attracting pollinators, favors the evolution of specialized pollination.

Interestingly, whereas it is sometimes thought that pollen-limited fruit set is a necessary prerequisite for the evolution of specialized pollination (e.g., Schemske 1983; Kiestler et al. 1984), pollen-limitation appears not to be important for fruit set in either *Yucca* species or in *L. schottii*. Pellmyr et al. (1996) have suggested that in the absence of pollen-limitation, differences among flower visitors in pollination quality (i.e., the genetic contribution to fruit set) can favor the evolution of specialized pollination through selective abortion of fruits of low genetic quality. Genetic analyses of ovules

in aborted vs. retained fruit in the yucca and senita systems are needed to test this prediction. While the mechanism promoting evolution of specialized pollination under resource limitation is not yet clear, it appears that pollen limitation is not a prerequisite for the evolution of obligate pollination mutualisms.

Despite their many similarities, the yucca and senita systems are characterized by a number of differences (Table 2). Three differences – variation in nectar production among plants, ability of moths to feed, and the presence of co-pollinators – suggest that the senita mutualism may be evolutionarily younger than the yucca mutualism. Continued selection for loss of nectar production in the senita cactus will further reduce the attractiveness of its flowers to co-pollinators. Alternatively, the apparent polymorphism in nectar production in senita may be evolutionarily stable because of selection pressures from effective diurnal co-pollinators visiting flowers to obtain pollen and nectar. Other differences, including a longer flowering season, several moth generations per season, and the presence of only one larva in a fruit in the senita system, suggest that the ecological and evolutionary dynamics of the two systems will differ, as discussed in detail by J.N. Holland and T.H. Fleming (submitted).

In conclusion, arid regions of North America appear to promote the evolution of obligate pollination mutualisms involving nocturnal moths and self-incompatible plants whose fruit set is resource limited. As predicted by Pellmyr et al. (1996), active pollination can evolve in a specialized pollinator in the presence of effective co-pollinators. Greater temporal reliability makes senita moths more effective pollinators than diurnal halictid bees. Oviposition on senita flowers and active pollination ties moth fitness to plant fitness through seed set. This reproductive connection lies at the heart of obligate pollination mutualisms, be they figs and fig wasps, yuccas and yucca moths, or senita cacti and senita moths.

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