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MUTUALISTIC INTERACTIONS BETWEEN *UPIGA VIRESCENS* (PYRALIDAE), A POLLINATING SEED-CONSUMER, AND *LOPHOCEREUS SCHOTTII* (CACTACEAE)

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Abstract. Pollinating seed-consuming interactions are rare, but include fig–fig wasp and yucca–yucca moth interactions, both of which are thought to be coevolved. Conditions favoring such mutualisms are poorly known but likely include plants and pollinators whose life cycles are synchronized. In this paper, we describe a new pollinating seed-consumer mutualism between a Sonoran Desert cactus, *Lophocereus schottii* (senita cactus), and a pyralid moth, *Upiga virescens* (senita moth). We compare this mutualism with the yucca mutualism in terms of life history traits, active pollination, and selective abortion. Senita cactus flowers were pollinated nearly exclusively by nocturnal senita moths, but a few halictid bees also pollinated flowers. Only 40% of flowers set fruit during the years of study, apparently due to resource limitation. All phases of the senita moth's life history were associated with the senita cactus. During flower visitation, female senita moths collected pollen, actively pollinated flowers, and oviposited one egg. After flowers closed, emerging larvae bored into the tops of developing fruit, where they consumed seeds and fruit tissue. However, not all seeds/fruit were consumed by larvae because only 20% of eggs produced larvae that survived to be seed/fruit consumers. Senita cactus and senita moth interactions were mutualistic. Moths received food resources (seeds, fruit) for their progeny, and cacti had a 4.8 benefit-to-cost ratio; only 21% of developing fruit were destroyed by larvae. Life history traits important to this mutualism included low survival of senita moth eggs/larvae, several moth generations per flowering season, host specificity of senita moths, active pollination, oviposition into flowers, and limited seed/fruit consumption. Active pollination by senita moths in the presence of co-pollinators supports the prediction that active pollination can evolve during a period of coexistence with co-pollinators. The specialization of both senita and senita moths in the presence of co-pollinators makes the senita mutualism quite remarkable in comparison with fig–fig wasp and yucca–yucca moth mutualisms.

Key words: life history; Lophocereus schottii; *mutualism; oviposition; pollination, active; seed consumption; senita cactus; senita moth; Sonoran Desert; specialization; survivorship;* Upiga virescens.

Introduction

Insects commonly oviposit in flowers and many insects pollinate flowers. However, oviposition in flowers and subsequent predispersal seed consumption by larvae of adults that pollinated flowers is extremely rare. Known cases of both pollinating and seed-consuming interactions between plants and their pollinators include *Silene vulgaris* and *Hadena* moths (Pettersson 1991*a*, Pettersson 1992*a*), *Lithophragma* and *Greya* moths (Thompson and Pellmyr 1992, Davis et al. 1992), *Trollius* spp. and globeflower flies (Pellmyr 1989, Pellmyr 1992), *Ficus* and fig wasps (Janzen 1979, Wiebes 1979), and *Yucca* and yucca moths (Riley 1892). Interactions between seed-consuming pollinators and plants confer a positive effect upon the pollinator population because adult pollinators assure food resources (i.e., seeds/fruit) for their progeny and in some cases obtain resources (i.e., nectar, pollen) for themselves. Based on net effects of the interaction on the plant population (usually measured as seed/fruit set), however, such interactions could potentially take the form of predation, commensalism, or mutualism.

Interactions between *Silene vulgaris* and *Hadena* moths are predatory due to ineffective pollination and larval consumption of seeds (Pettersson 1991*a*, *b*). *Greya politella* moths are effective pollinators but are commensalistic with *Lithophragma* in years or populations where co-pollinators are abundant because their positive effects on seed set are masked by co-pollinators (Thompson and Pellmyr 1992, Pellmyr et al. 1996). In contrast, the other three known pollinating seed-consuming interactions are mutualistic, and each has been referred to as a highly specialized, coevolved system: (1) *Trollius europaeus* and *Chiastocheta* flies (Pellmyr 1989, 1992), (2) figs and fig wasps (Janzen 1979, Wiebes 1979, Bronstein 1987, Kjellberg et al.

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1987, Addicott et al. 1990), and (3) yucca and yucca moths (Riley 1892, Aker and Udovic 1981, Addicott 1986, Pellmyr et al. 1996). *Trollius europaeus* interacts mutualistically with three species of *Chiastocheta* flies that pollinate and oviposit into flowers (Pellmyr 1989, 1992). Actively pollinating fig wasps (Herre 1996, Machado et al. 1996, West et al. 1996, Anstett et al. 1997) are mutualistic with *Ficus* because wasps assure a food resource for progeny and simultaneously confer a positive effect on seed set. Similarly, *Yucca* interact mutualistically with yucca moths that actively pollinate flowers and oviposit into locules where larval growth and development occur. Fig–fig wasp and yucca–yucca moth mutualisms differ from other seed-consuming pollination interactions in that high plant specificity occurs among pollinators and co-pollinators are absent (Miles 1983, Bronstein 1987, Addicott et al. 1990, Pellmyr and Thompson 1992, James et al. 1993), and in that pollen collection and pollination are active, not passive (e.g., Riley 1892, Bronstein 1992, Pellmyr 1997).

Studies of specialized pollination mutualisms indicate that the community context in which pairwise interactions occur between plant and pollinator can affect the outcome of interactions in part due to the presence or absence of co-pollinators and predators of pollinators (Pellmyr 1989, 1992, Thompson and Pellmyr 1992, Herre 1996, West et al. 1996, Thompson 1997). In addition to community context, life history traits are increasingly recognized as important for understanding the outcome of population interactions in communities (Addicott et al. 1990, Bronstein 1994, Polis et al. 1996). In order for a plant and pollinator to develop an obligate mutualism, appropriate life history traits must be present in plant and pollinator populations (Addicott et al. 1990, Waser et al. 1996). Specialization of a plant on a pollinator is predicted to occur when the plant is (1) large and long lived, (2) has many reproductive episodes, and/or (3) has an effective pollinator whose population dynamics are predictable (Waser et al. 1996). Specialization of a pollinator on a plant is predicted to occur when (1) the pollinator's generation time is not longer than the duration of a flowering season and (2) synchrony occurs between flowering phenology and a pollinator's life cycle (Addicott et al. 1990, Waser et al. 1996).

In this paper, we report a mutualism involving pollination and seed-consumption interactions between a pyralid moth (*Upiga virescens*) and a columnar cactus (*Lophocereus schottii*), and the third known occurrence of active pollination. Results of this study enabled us to evaluate theory on the importance of life history traits in the ecology and evolution of pollinating seed-consuming mutualisms by comparing the senita mutualism with other such mutualisms. Specifically, we studied (1) phenology, seed set and seed germination in *L. schottii*, (2) patterns of flower visitation and flower visitation behavior of *U. virescens*, (3) oviposition by *U. virescens* on flowers of *L. schottii*, and (4) survivorship, life cycle, and life stage associations between *U. virescens* and *L. schottii.*

METHODS

Study species and study area

The genus *Lophocereus* contains two species that are restricted to the Sonoran Desert, with populations of *L. schottii* (Englem.) extending as far north as southern Arizona (Lindsay 1963). The senita cactus attains heights of 2–4 m (Parker 1989) and has many branches radiating from its base. Senita produce small whitish-pink flowers that were presumed to be hawk moth pollinated (Gibson and Horak 1978). Cactus branches bear many areoles (spine-bearing pads) that can produce one or more flowers per night. Flowers open at sunset and remain open for 6–12 h. Each flower contains a single stigma and 109 ± 4.9 anthers (mean ± 1 SE; $n = 30$ plants). Corollas are 6.1 ± 0.2 mm ($n = 30$ plants) wide at the mouth of the flower, 9 mm long, and 2.1 ± 0.1 mm ($n = 30$ plants) wide just above the ovary. *Lophocereus schottii* is self-incompatible and reproduces both vegetatively and sexually (Parker 1989, Fleming and Holland 1998).

The senita moth, *Upiga virescens* (Hulst) (Lepidoptera: Pyralidae), is the only known species of *Upiga* (Munroe 1972). Its range includes southern Arizona and Sonora and Baja California, Mexico. It is a small moth with a forewing length of 7–9 mm. The last abdominal segments of females are covered ventrally with many long scales (Fleming and Holland 1998).

We conducted this study from April through July in 1995 and 1996 on the Gulf of California (29° N, 110° W) ~9 km northeast of Bahia Kino, Sonora, Mexico. Annual rainfall at Bahia Kino is 200 mm. Topography of the area includes sandy flatlands and steep hills (200–450 m above sea level). Study sites (Seri and Polilla Flats) were 2 km apart with adult *L. schottii* densities of 7 and 20 plants per hectare, respectively. For further description of the Central Gulf Coast region of the Sonoran Desert and our study site, see Shreve and Wiggins (1964) and Fleming et al. (1996).

Flower phenology, nectar production, and seed set

We studied flower phenology of *L. schottii* for the same 20 plants in 1995 and 1996 by counting the number of open flowers at 1-wk intervals, beginning the first week of April. Our observations of flower phenology stopped in early July, about three-quarters through the flowering season. In 1996, we measured floral nectar using 2-μL capillary tubes for $n = 56$ bagged and $n = 54$ unbagged flowers among 29 cacti. Bagged flowers were covered with bridal-veil netting (1-mm mesh) before opening; the next morning, netting was removed and nectar measured. To determine the number and viability of seeds resulting from pollination, we collected three fruits from each of 30 plants and counted seeds. We assessed seed viability by placing all seeds from a fruit on moistened filter paper in a petri dish and counting the number of seeds that germinated within 12 d. Mean number of seeds per fruit and percentage germination per fruit were calculated by averaging the means of 30 plants. We conducted pollinator exclusion and hand-pollination studies to determine the contribution of nocturnal (senita moths) and diurnal (bees) pollinators to fruit set and whether fruit set was limited by pollen. Pollinator exclusion studies included three treatments (Fleming and Holland 1998): (1) control flowers open to all pollinators, (2) nocturnal flowers available to pollinators at night but covered with bridal-veil netting before sunrise, and (3) diurnal flowers available to pollinators in the morning but covered with bridal-veil netting during the night. Stigmas of hand-pollination flowers received fresh pollen from another plant. Hand-pollination flowers were not covered with netting.

Moth activity period and flower visitation

We determined activity periods and time of flower visitation of senita moths by conducting hourly censuses of flowers on each of six nights. We counted the total number of flowers on each of 30 plants and censused a subset (~1–100 flowers per plant) of flowers on each plant to determine the proportion of flowers occupied by senita moths. Censuses began in the evening at 1900 MST and ended at 2400 or 0100, when <5% of flowers were occupied by moths. During each census, senita moth matings were noted and all flower visitors (senita moths and others) were recorded. All proportions were arcsine square-root transformed prior to statistical analysis. Repeated-measures ANOVA was used to test for the effect of time on proportion of flowers occupied by moths. Linear regression analyses were used to determine whether peak proportions of flowers occupied by moths were associated with total number of flowers on a plant. We studied moth behavior during flower visitation by observing focal flowers after dark between 2000 and 2300. When a moth arrived at a flower, we recorded the sequence of its behaviors and duration of each behavior to the nearest second. Observations of flower visitation behavior ceased when moths either left a flower or remained in a nectaring position for >1 h. We recorded 240 individual behaviors by 94 moths during 22.8 h of observation.

Moth life stages and survivorship

On six nights for 30 plants, we counted the total number of flowers per plant and the number of eggs on accessible flowers, in order to determine (1) distribution of eggs among flowers in the cactus population and (2) proportion of flowers per plant receiving an egg. We marked two cohorts (*A* and *B*) of *U. virescens* eggs by tagging flowers containing an egg to study survivorship, life stage associations with *L. schottii*, and agents of mortality. Our studies of the two cohorts were staggered in time; we marked cohort *B* after completing the study of cohort *A*. For cohort *A* we tagged 229 flowers bearing an egg and then randomly collected a subset (9–35) of the flowers/fruits over 9 d. We did not follow cohort *A* through pupation because cohort size was too small to allow for sequential destructive sampling for >9 d. For cohort *B*, we tagged 589 flowers bearing an egg and then randomly collected a subset (12–72) of flowers/fruits/areoles over 28 d. For each collection we dissected corollas, fruits, and/or areoles to determine the presence of *U. virescens*. Survivorship was determined based on population proportions (Varley et al. 1973), and standard deviations of population proportions were calculated. To further quantify larval presence in cactus branches, we dissected the terminal 35 cm of eight cactus branches from eight plants. For each branch we counted the number of reproductive areoles ($n = 1375$ areoles), number of larval galleries behind areoles, and determined the presence or absence of a parasitic wasp based on wasp pupa or pupal case. To determine if larval pupation occurred in aborted fruit in the field, we collected and dissected $n = 783$ aborted fruits from underneath $n = 28$ cacti and examined them for presence or absence of larvae, pupae, or pupal cases.

RESULTS

Phenology of Lophocereus schottii

Lophocereus schottii flowered from the first week of April through at least early July (Fig. 1), and usually flowers through early August (Shreve and Wiggins 1964). In both 1995 and 1996, mean flower production was <10 flowers per cactus per night prior to mid-April and >40 flowers per cactus per night by July (Fig. 1). Although differences in peaks and troughs of flower production occurred between years, overall phenological pattern and rate of flower production were similar for the two years. Flower density did not differ between 1995 (22.5 ± 4.8 flowers per plant per census ($n = 14$ wk) and 1996 (25.2 ± 5.7 flowers per plant per census, $n = 13$ wk) flowering seasons (means ± 1 SE) ($t = 0.37$, df = 24, $P = 0.72$). If we extrapolate our phenology results through August, each plant in the population produced an average of 3138 ± 545 (range 291–10 861) and 3370 ± 522 (196–8867) flowers per season in 1995 and 1996, respectively.

Senita flowers opened shortly after sunset (~2000 Mountain Standard Time [MST]) and remained open for 6–12 h. In 1995, which had a cool spring, flowers frequently remained open after sunrise (~0500) until 0900. However, during the warmer spring of 1996 flowers were closed by 0400 in the morning, >1 h before sunrise. In 1995 and 1996, respectively, pollinator exclusion experiments indicated that 75 and 90% of fruit set resulted from nocturnal pollination by *Upiga virescens*; the remaining 10–25% resulted from pollination by diurnal co-pollinators (Fleming and Holland

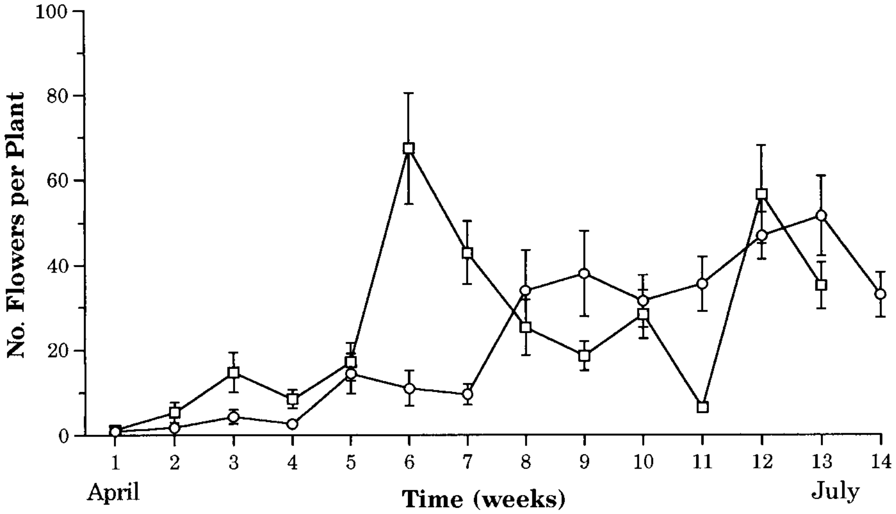

FIG. 1. Flower phenology (no. flowers per plant [mean ± 1 SE]) of *Lophocereus schottii* in 1995 (○) and 1996 (□). Flower censuses occurred from the first week of April through early July. The same 20 plants were censused every week in both years.

1998). Hand-pollination experiments indicated that fruit set was apparently resource limited in 1995 and 1996, with >50% of fruit aborting by day six (Fleming and Holland 1998).

Nectar production and seed set

Nectar production was variable among plants within the cactus population. Both bagged and unbagged flowers produced nectar and lacked nectar (Fig. 2). For bagged flowers that contained nectar, flowers most frequently produced 0.50–0.74 μL of nectar (Fig. 2). Of the 20 plants where nectar was measured for >1 bagged flower, all flowers measured for 10 plants lacked nectar while all flowers for the other 10 plants contained nectar. In other words, individual cacti had flowers that either contained nectar or lacked nectar. Bagged flowers lacking nectar suggested that not all plants within the cactus population produced nectar. Alternatively, the polymorphism in the population could be for reabsorption of nectar prior to flower closing. Nonetheless, neither the presence nor volume of nectar served as a reliable resource to attract co-pollinators.

Fruit matured in ~30 d and contained small black seeds weighing 2.7 ± 0.07 mg (mean ± 1 SE). In each

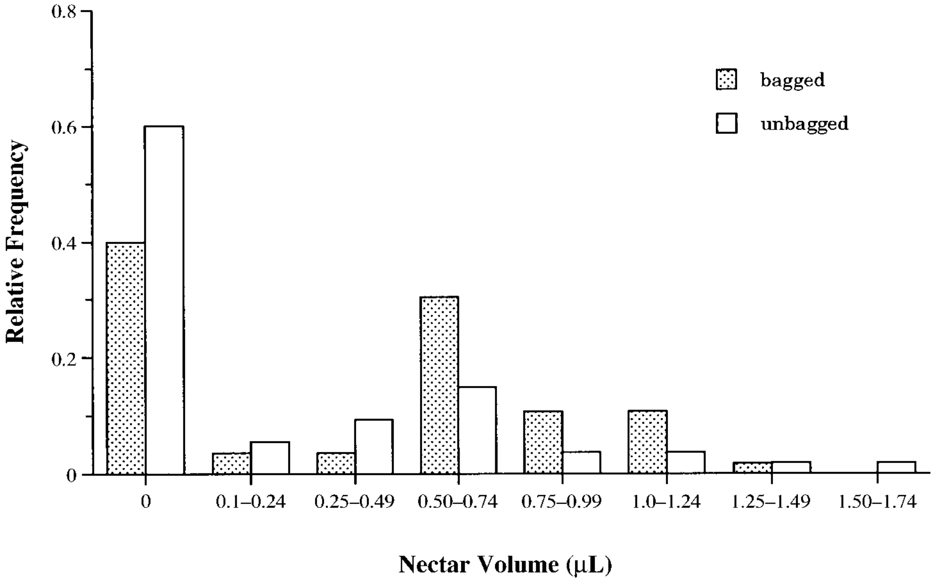

FIG. 2. Relative frequency of nectar volume for bagged (*n* = 56 flowers across 29 plants) and unbagged (*n* = 54 flowers across 29 plants) flowers within the cactus population.

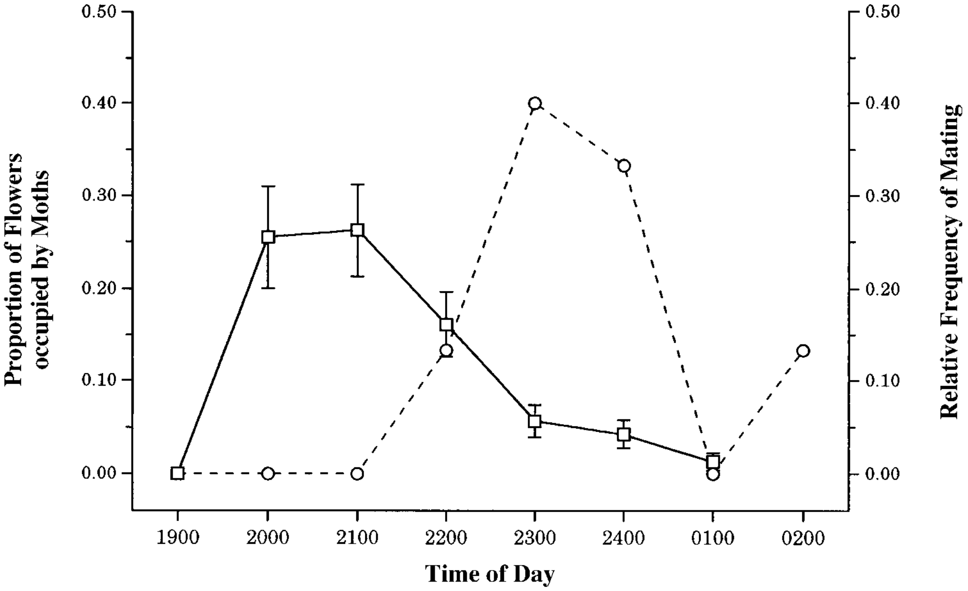

FIG. 3. Activity period of *Upiga virescens.* Proportion (mean ± 1 SE) of flowers occupied by moths (□) every hour for each of six nights and the relative frequency of observed moths that were mating (○, $n = 15$ moth matings) during the night.

fruit, an average of 182 ± 11 seeds (range 84–340 seeds) set. Of those seeds in each fruit, 97.5 ± 0.54% germinated.

Life history of Upiga virescens

Activity period.—During the day, moths rested on the 5–10 cm long spines of senita branches. Moths began to visit flowers when they opened at 2000 (Fig. 3). On six nights, proportion of flowers occupied by moths ranged from <10% to 45%. Occupancy peaked at 2000 and 2100 and declined steadily thereafter, approaching zero at 0100 (Fig. 3). Proportion of flowers occupied by moths varied significantly during the night ($F_{5,25} = 21.52$, $P < 0.0001$; Fig. 3). Peak proportion of flowers occupied by moths was not correlated with number of open flowers per plant on any of six nights ($r^2 < 0.10$ and $P > 0.05$ for each night). Plants producing a greater number of flowers did not necessarily attract a proportionately greater number of moths.

Adults.—Primary events during the adult life stage of *U. virescens* were flower visitation and mating. Relative frequency of mating increased as the proportion of flowers occupied by moths decreased through the night (Fig. 3). All mating events were observed on senita cactus spines with the peak occurring between 2300 and 2400. Flowers were visited mostly by female moths: of 50 moths collected from flowers, only two were males. Sex ratio of adults collected at night on senita plants but not in flowers did not differ significantly from 1:1 ($n = 119$ adult moths; $\chi^2 = 2.72$, $P > 0.10$). Flower visitation consisted of one or more of five behaviors: pollen collection (1.5 ± 0.38 min [mean ± 1 SE]), active pollination (0.45 ± 0.10 min), nectaring (14.6 ± 3.21 min), resting (7.9 ± 2.26 min), and oviposition (1.5 ± 0.96 min). Female moths actively collected pollen by lowering and rubbing their abdomens among anthers. Females actively pollinated flowers by climbing onto the stigma in a head down position and rubbing their abdomen onto the stigma, thereby transferring pollen from abdomen to stigma. Female moths have a ''pollen brush'' on their abdomens (for illustrations, see Fleming and Holland [1998]) that facilitates pollen collection, transport, and delivery to the stigma. When (presumably) consuming nectar, moths crawled deep into the corolla and remained there from 30 s to >1 h. Ovipositing moths bent and rubbed their abdomen on the flower, and then deposited an egg on the upper surface of a petal tip or among anthers. When flowers closed, eggs were located inside wilting corollas.

Eggs.—Eggs were uniformly distributed across flowers on five of six nights of observation (Table 1). Fewer flowers contained zero eggs than expected, many more flowers contained one egg than expected, and fewer flowers contained two or three eggs than expected (Table 1). Thus, moths avoided ovipositing more than one egg per flower. Of flowers receiving an egg, 94% had only one egg while 6% had >1 egg. On two nights of egg censusing at Polilla Flats, 22.4 ± 4.6% and 19.7 ± 3.4% (mean ± 1 SE) of flowers received an egg ($n = 30$ plants); on four nights of egg censusing at Seri Flats, 43.7 ± 3.1, 39.4 ± 3.2, 37.1 ± 2.9, and 33.2 ± 3.7% of all flowers contained eggs ($n = 30$ plants).

Larvae.—Larvae hatched from eggs within 3 d of oviposition and began to enter fruit as early as 3 d. After hatching, larvae moved through the wilting corolla toward the ovary; larvae entered fruit by boring a hole through the base of the corolla into the top of

TABLE 1. Observed (O) and expected (E) distribution of moth (*Upiga virescens*) eggs on senita cactus (*Lophocereus schottii*) flowers, and estimated dispersion patterns (s^2/μ).

		0 Eggs		1 Egg		2 Eggs		3 Eggs					
Date†	Site	O	E	O	E	O	E	O	E	χ^2	df	*P*	s^2/μ
960603	Polilla	111	115.3	40	31.9	1	4.4	0	<1.0	5.28	1	<0.025	0.77
960604	Polilla	95	93.9	26	27.6	4	4.0	1	<1.0	0.16	1	>0.650	0.93
960604	Seri	267	292.4	180	131.9	9	29.7	3	4.5	35.1	2	<0.001	0.72
960624	Seri	413	446.4	249	185.9	12	38.7	3	5.4	43.8	2	<0.001	0.73
960625	Seri	412	435.4	201	157.4	11	28.4	1	3.4	26.1	2	<0.001	0.74
960626	Seri	326	339.0	133	109.4	9	17.6	0	1.9	11.9	2	<0.003	0.80

Note: When expected values were <1.0, the tails of the distribution were summed, and χ^2 calculated based on three terms (0, 1, ≥2 eggs) instead of four (0, 1, 2, 3 eggs).

† Dates are given as yymmdd; i.e., 960603 indicates 3 June 1996.

young fruit. Although more than one egg was observed on flowers and two larvae occasionally occurred in corollas, only one larva entered a fruit to consume developing seeds and fruit wall tissue. Upon arriving at the bottom of fruit, larvae made an exit hole at the point of fruit-to-areole attachment. They then bored a hole into the areole and consumed tissue beneath the areole, creating a small gallery in the cactus branch. Of 1375 reproductive areoles examined, 21% contained larval galleries and 2.3% of areoles had >1 gallery, indicating that larval galleries did not render areoles incapable of further flower or fruit production (Table 2).

Creation of an exit hole in a fruit always resulted in abscission of the fruit. Thus, while larvae consumed only a fraction of developing seeds in fruit, larval-induced fruit abscission ultimately resulted in total seed mortality for fruit that contained a larva. All flowers containing an egg did not necessarily abscise because survivorship of eggs and early instar larvae was low (see *Survivorship*, below). Thus, not all fruit of flowers pollinated and oviposited on contained a larva. Of 589 flowers containing eggs, 67% set fruit and 21% of fruit abscised due to larvae, providing the cactus with a 4.8 benefit-to-cost ratio for interacting with *Upiga virescens.*

Pupae.—Galleries created by larvae in cactus branches were used as pupation chambers. To determine if pupation occurred in aborted fruit, fruit containing a larva were brought into the laboratory (n = 10 fruits). Although all larvae remained in the fruit and pupated, not all adults emerged from fruit because fruit harden during the pupation period. Although adults pupated and emerged from fruit in the laboratory, no pupal cases were observed in aborted fruit collected in the field (n = 783 fruits from 30 plants), and only one of 783 aborted fruits contained a larva. Thus, *U. virescens* does not pupate in aborted fruit nor do larvae commonly occur in aborted fruit in the field.

TABLE 2. Larval/pupal environment of the moth *Upiga virescens* on the senita cactus, *Lophocereus schottii,* in the Sonoran Desert.

Statistic	Branches per cactus	Areoles per branch	% Areoles with gallery	% Galleries with wasp
Mean	40 ± 3	172 ± 11	21.4 ± 6.6	16.6 ± 2.4
Range	16–89	111–213	4.5–64.2	5.6–25.3

Notes: Data in first row are means ± 1 SE. Sample sizes: number of branches per cactus (n = 30 plants), number of areoles per 35 cm of branch (n = 8 plants), percentage of areoles with larval gallery per cactus branch (n = 8 branches), and percentage of larval galleries per branch with parasitic wasp (n = 8 branches).

Survivorship.—Less than 20% of *U. virescens* larvae survived to 6 d of age; survival was relatively constant from 6 d to pupation (Fig. 4). Four factors contributed to preadult survivorship in *U. virescens*: (1) low proportion of eggs hatching, (2) corolla-induced mortality, (3) resource-limited fruit abortion, and (4) wasp parasitism. Low survival of eggs due to predation and/or low fertility accounted for the greatest mortality for both cohorts (Fig. 4). For cohorts *A* and *B,* respectively, only 33 and 26% of eggs produced larvae. Since eggs were not oviposited directly into flower ovaries as usually occurs with yucca moths (Riley 1892, Aker and Udovic 1981; some yucca moths oviposit into floral pedicels and into petals [see Davis 1967]), eggs were exposed to abiotic (e.g., desiccation) and biotic (e.g., predation) agents of mortality.

Survival during days two through six was a function of both corolla-induced mortality and fruit abortion. Larvae need to reach the base of corollas before day six, because corollas wilt and harden after flowers close, providing an unfavorable environment for larvae. As indicated by the increase in proportion of dead larvae in corollas after day five of fruit maturation (Fig. 4), larvae that fail to exit corollas before day six die, likely due to their inability to eat through the base of hardened corollas. For cohorts *A* and *B,* respectively, 35 and 17% of larvae died within corollas. In addition, *L. schottii* flowers not setting fruit were aborted during the first 6 d after flowering (Fig. 5). Consequently, even if larvae hatch from eggs, a proportion of larvae (determined by percentage fruit set) nevertheless dies due to fruit abortion. For cohorts *A* and *B*, respectively, 42 and 67% of flowers with an egg set fruit. Thus, of larvae hatching from eggs, 58 and 33% died due to resource-limited fruit abortion. Low egg hatching, corolla

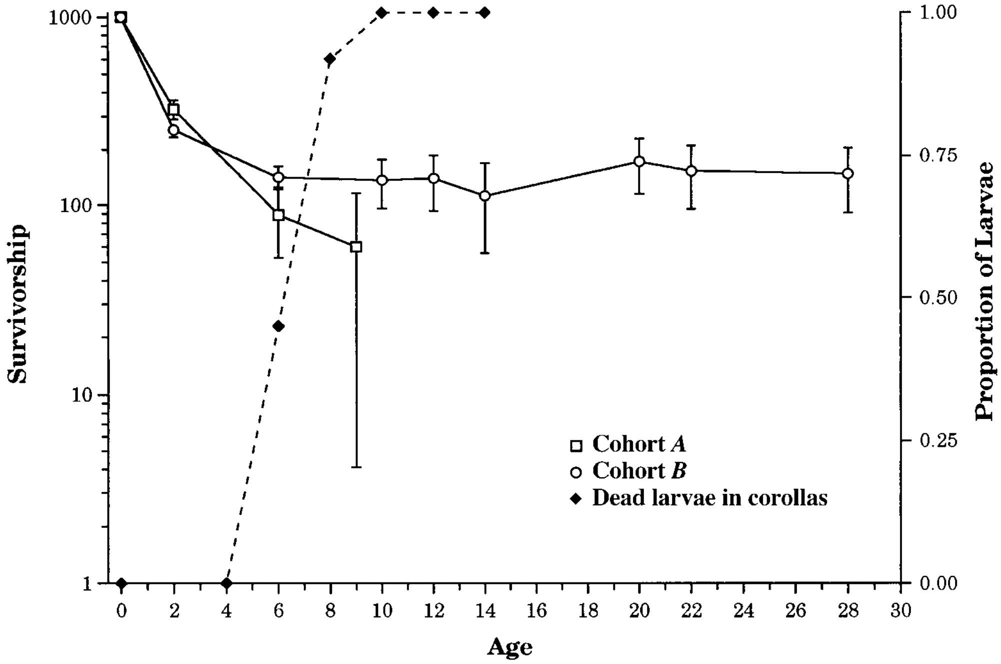

FIG. 4. Age-specific survivorship (mean ± 1 SD of population proportion) of two *Upiga virescens* cohorts, *A* (n = 229 individuals) and *B* (n = 589 individuals), and the proportion of dead larvae observed (n = 49 larvae) in corollas.

deaths, and limited fruit set accounted for mortality up to day six for cohorts *A* and *B* (Fig. 4).

Survival of *U. virescens* remained relatively constant from day six until pupation, with ~20% of eggs producing larvae that reach pupation. Of larvae reaching pupation in cohort *B,* 12% were parasitized by an endoparasitic wasp. Furthermore, of the 21% of areoles containing a gallery, 17% of larval galleries contained a wasp pupa or pupal case instead of a *U. virescens* pupa or pupal case (Table 2). Thus, 12–17% of larvae that survive to pupation are killed by a parasitic wasp. Adult moths were killed by spiders that spin webs among cactus branches. In summary, ~17% of a cohort of *U. virescens* survived through pupation. In comparison to the 1% survival to the adult life stage for the spruce budworm (Morris et al. 1958) and winter moth (Varley et al. 1973), the senita moth has a relatively high survival rate.

Other flower visitors

When flowers remained open after sunrise in 1995, they were visited and pollinated by halictid bees (*Augochlorella* sp. and *Agapostemon* sp.). The primary nocturnal flower visitor was *U. virescens,* but occasionally flowers were visited by other arthropods, including: Neuroptera (Hemerobiidae), Orthoptera (Gryllacrididae), Coleoptera (Alleculidae, Cerambycidae, Cleridae, Tenebrionidae), Lepidoptera (Pyralidae), and Araneae. Flower visitation by organisms other than *U. virescens* was rare: of 19 h and 7660 separate obser-

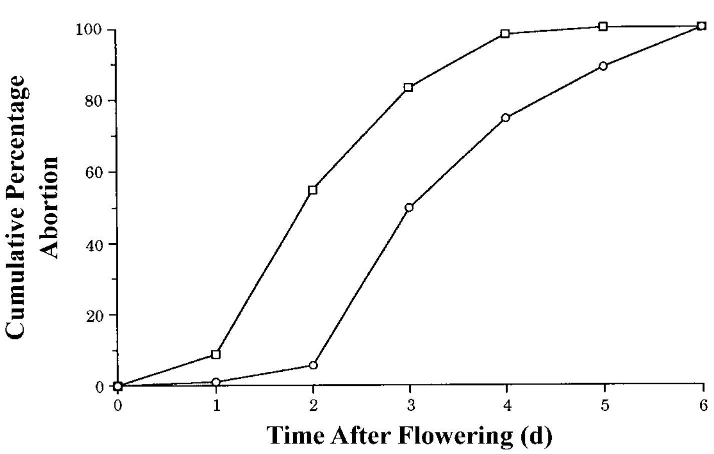

FIG. 5. Cumulative percentage abortion of senita fruit during the 6 d of fruit abortion following flowering in two separate studies (□, n = 113 fruits; ○, n = 197 fruits). After day 6, fruits abscise but do not abort. Larvae may begin to enter fruit at day 3, but seed consumption by larvae did not occur before the larval age of 5 d.

vations of flowers, only 1.2% of observations yielded insects other than *U. virescens.* These arthropods behaved in a manner that would not facilitate pollination, but instead were flower/fruit herbivores and pollen consumers. The only other Lepidoptera visiting flowers, *Cactobrosis fernaldialis* (Pyralidae), was uncommon. Adults were not observed probing for nectar, but instead were only observed sitting on flower petals. Larvae of *C. fernaldialis* utilized ~3% of senita fruits as a food resource, but there was a temporal separation from *U. virescens* in fruit occupancy. Larvae of *C. fernaldialis* did not enter fruit prior to day 14, 2–4 d after senita larvae entered cactus branches. Larvae of *C. fernaldialis* bored into the fruit from the outside and then consumed all seeds before emerging from the fruit to pupate elsewhere.

DISCUSSION

This study reports a mutualism between the senita cactus and senita moth, an active pollinator whose progeny consume seeds of flowers pollinated by the adult. Female senita moths are the third known pollinator to oviposit an egg onto flowers, actively collect pollen, and actively pollinate flowers during flower visitation. Like other Lepidoptera (Thompson and Pellmyr 1991, Dempster 1992, Pettersson 1992*b*), female senita moths avoided ovipositing eggs in flowers that already contained an egg (Table 1). Eggs hatched within 3 d of flower closing and larvae crawled down the wilting corolla and bored into the top of fruit, where they consumed fruit before entering the cactus branch to pupate. Not all fruits pollinated by moths were destroyed by their larvae, because egg and larval survivorship to 6 d was low: only a fraction of eggs produced larvae that survived to become seed consumers. Benefit-to-cost ratio for *Lophocereus schottii* interacting with senita moths was 4.8 (~21% of fruit destroyed by larvae), and is consistent with the fact that 21% of areoles contained a larval gallery (Table 2) and that only 20% of *Upiga virescens* survive to day six (Fig. 4). Benefits of *U. virescens* to pollination and fruit set in *L. schottii* are thus >3–4× the costs of seed mortality induced by larvae, which is comparable with the yucca mutualism (Addicott 1986, Powell 1992).

Comparison with other pollination–seed-consumption interactions

The senita and senita-moth mutualism is the sixth known case of interaction of pollination with seed consumption; other cases include figs and fig wasps, yucca and yucca moths, *Trollius europaeus* and *Chiastocheta* flies, *Lithophragma* and *Greya* moths, and *Silene* and *Hadena* moths. If our findings of the senita mutualism generalize to most years and populations, then senita cactus and senita moth interactions are most ecologically and evolutionarily similar to the pollinating seed-consuming interactions of yucca and fig mutualisms. In all three mutualisms, (1) both plant and pollinator populations specialize on one another, (2) interactions are mutualistic and apparently coevolved, (3) pollinators oviposit eggs into flowers, and (4) pollinators actively pollinate flowers. However, one substantial difference occurs between the senita mutualism and the fig and yucca mutualisms that relates to the community context in which the interaction occurs: absence or presence of co-pollinators. Co-pollinators are absent from fig and yucca mutualisms, where fruit set is dependent upon one or two species of pollinators (Bronstein 1987, James et al. 1993, Addicott and Tyre 1995). In contrast, co-pollinators are still present, but uncommon, in the senita mutualism and are not completely excluded by senita cacti.

Presence of co-pollinators is a similarity between the senita mutualism and interactions between *Lithophragma* and *Greya* moths. In years or populations where co-pollinators are abundant, *Lithophragma* and *Greya* interactions are commensal because *Greya* produce no net negative or positive effect on seeds matured in *Lithophragma* (Thompson and Pellmyr 1992, Pellmyr and Thompson 1996). Conversely, when co-pollinators are absent, rare, or unpredictable, *Lithophragma* and *Greya* interactions may be mutualistic because effects of *Greya* on seed set are not masked by co-pollinators (Thompson and Pellmyr 1992). Whereas the outcome and specialization of *Lithophragma–Greya* interactions depend on the year, population, and community context (i.e., co-pollinators) of interactions (Thompson and Pellmyr 1992, Pellmyr and Thompson 1996), the presence of co-pollinators has not altered the outcome of senita cactus and senita moth interactions for different populations or years of study. This study and another at Bahia Kino (Fleming and Holland 1998) found senita cactus and senita moth interactions to be mutualistic, and a third study (J. N. Holland and T. H. Fleming, *unpublished data*) conducted in south-central Arizona in 1997 found senita interactions to be mutualistic in three different populations. Thus, in all three studies senita moth and senita cactus interactions were mutualistic and unaltered by the presence of co-pollinators. Presence of effective co-pollinators in communities may prevent specialization of *Lithophragma* populations on pollination by *Greya* moths. In contrast, presence of effective co-pollinators has not prevented specialization between *L. schottii* and *U. virescens,* because, unlike co-pollinators of *Lithophragma* (Thompson and Pellmyr 1992), co-pollinators of senita cacti generally have been rare and/or temporally unreliable.

Effects of life history traits on maintenance of mutualism

Necessary traits for the evolution of obligate pollination mutualism between yucca and yucca moths included (1) local host specificity of pollinators, (2) oviposition into flowers, (3) partial seed consumption, and (4) behavior that facilitates pollination (Pellmyr et al. 1996). The senita mutualism is similar to the yucca mutualism in that it exhibits traits necessary for the ecological and evolutionary maintenance of an obligate pollination mutualism. *Upiga virescens* is host specific. Our observations of flowers and fruits of other cactus species have not revealed senita moths or larvae; in contrast, the other pyralid (*Cactobrosis fernaldialis*) that parasitizes senita fruit is not locally host specific. Its larvae occur in buds and fruit of organ pipe, saguaro, and senita cacti (Steenbergh and Lowe 1977; J. N. Holland, *personal observations*). In addition to host specificity, senita moths oviposit into flowers and actively pollinate flowers, and senita larvae only consume part of the seed crop pollinated by adult moths. While *U. virescens* is an obligate mutualist, *L. schottii* is at the interface between an obligate and a facultative mutualist because pollination and seed set sometimes result from co-pollinators.

Number of moth generations per flowering season should reflect duration of flowering season in specialized pollination mutualisms (Waser et al. 1996). In the yucca mutualism, flowering season ranges from 2–3 d to 3–6 wk with moths having just one generation per flowering season. Senita cacti flower for up to 20 wk and senita moths have several generations per flowering season. Yucca and senita mutualisms thus differ in the duration of flowering and number of moth generations per season, but they are similar in that within each mutualism the number of moth generations reflects the duration of the flowering season. The strong association between all life stages of *U. virescens* and senita cacti should allow for moth population dynamics and flowering season to be synchronized (Waser et al. 1996).

Along with plant specificity, mating on plants, oviposition on flowers, partial seed consumption, and pollination behavior (Pellmyr and Thompson 1992, Pellmyr et al. 1996), survivorship is another important life history trait that contributes to the maintenance of obligate pollination mutualisms. Because a one-to-one relationship occurs between senita larval survival and the cost to the plant (i.e., fruit/seed mortality), an increase in the survivorship of larvae could alter the net outcome of senita cactus and senita moth interactions. For example, increasing larval survival to day 10 by 30% (i.e., increased egg hatching and/or reduced corolla and fruit abortion deaths) would shift the outcome of interactions from mutualism to commensalism or predation for that particular cohort of moths. For senita and senita moth interactions, it is the high benefit to plants from pollination by moths and the low survivorship of moth larvae that maintains the high benefit-to-cost ratio for the plant. The generality of low survivorship as a necessary life history trait in maintaining the mutualistic outcome of interactions between seed-consuming pollinators and plants is unknown, since data are lacking on the survivorship of other similar mutualists. Nonetheless, we predict that survival is low in egg and early instars of yucca moths, and that increased survival could alter the outcome of yucca and yucca moth interactions. Furthermore, resource-limited fruit production, a common life history trait of senita, yucca, and some fig plants (Bronstein 1988, Pellmyr and Huth 1994, Herre 1996, Huth and Pellmyr 1997, Fleming and Holland 1998; J. N. Holland and T. H. Fleming, *unpublished data*), is important to survival of larvae but its ecological importance to the mutualistic outcome remains unknown and warrants further investigation.

On selective abortion and active pollination in obligate pollination mutualisms

In the yucca mutualism, selective abortion of fruits containing large egg/larval loads should occur when resources limit fruit set. Selective abortion in yucca simultaneously reduces costs to yucca plants and maintains moth populations, since other yucca fruits with low egg/larva numbers are retained. Selective abortion in yucca appears to be a mechanism inhibiting overexploitation by yucca moths (Pellmyr and Huth 1994, Richter and Weis 1995, Huth and Pellmyr 1997). However, senita fruits only contain one larva each; no continuum of larval infestation occurs (i.e., high to low egg/larva load per fruit) as in yucca fruit (Pellmyr and Huth 1994). Thus, criteria for selection of fruit to abort would have to be presence or absence of a larva in a fruit. If such criteria were the basis for selective abortion, and senita cacti selectively aborted fruit with a larva, then population interactions would be destabilized since selectively aborting senita fruit containing a larva would result in moth population extinction. In addition, resource-limited fruit abortion occurs up to 6 d after flower closing (Fig. 5), and not during the subsequent 20 d of fruit maturation. During these 6 d, larvae have just begun to enter fruit and seed consumption has not yet occurred. Hence, selective abortion by senita cacti would have to be based on some factor other than seed consumption. This appears to be the case in the yucca mutualism, where yucca fruit abort prior to seed consumption by larvae (Pellmyr and Huth 1994). For the yucca mutualism, this is a paradox because yucca differentially abort fruit with large numbers of eggs/larvae but the mechanism for selective fruit abortion is not based upon larval seed consumption (Pellmyr and Huth 1994).

Selective abortion of fruit as a mechanism to reduce overexploitation in senita moths likely does not occur, but selective abortion of fruit based on pollination quality and quantity is plausible since this provides a strong selective pressure for the evolution of active pollination (Pellmyr and Huth 1994, Pellmyr et al. 1996). Flowers with greater pollination quality and quantity would be preferentially retained by plants where resources limit fruit production, thus increasing progeny survival of moths that actively pollinate. The three known active pollinators, fig wasps, yucca moths, and senita moths, have specialized morphological and behavioral traits that increase the effectiveness of pollen collection, transport, and delivery to the stigma. Active pollination, and associated morphological and behavioral traits, can be selected for in a pollinator population when a small number of co-pollinators are present and the behavior does not require any counteradaptation on the part of the plant (Pellmyr and Huth 1994, Pellmyr et al. 1996). Active pollination in senita moths supports such a proposition since co-pollinators are present. The senita mutualism appears to be the first documented case of the evolution of active pollination in the presence of co-pollinators. Reduction in and lack of nectar production in the senita cactus (Fig. 2) allow for specialization on senita moths by discouraging co-pollinators that visit flowers for nectar rewards, and reduced nectar production conserves energy for use in fruit production in populations where fruit set is resource-limited (Pellmyr et al. 1996).

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