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Discrimination among floral resources by an obligately pollinating seed-eating moth: host-marking signals and pollination and florivory cues

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ABSTRACT

Background: For oviposition, some insects exploit small discrete food items from which their larvae then develop but do not disperse. In particular, senita moths exploit senita cacti by obligately pollinating and ovipositing floral resources. Larvae consume the fruit but do not disperse among them. Previous studies have shown that moth oviposition occurs in a non-random, uniform distribution among floral resources (one egg per flower).

Question: Do host-marking pheromones of senita moths, pollinated stigmas, and florivory act as signals and cues that aid them to avoid ovipositing in the previously exploited floral resources?

Methods: We measured rates of moth pollination and oviposition of flowers in a series of experiments. In one experiment, we simulated pheromone deposition by placing an extract of moth abdomens on flowers. In another, we compared oviposition rates on hand-pollinated flowers with those on controls. In a third, we simulated florivory by damaging stigmas, anthers or petals.

Results: Moth exploitation of floral resources was higher for control than abdomen-extract flowers. Control flowers received more ovipositions than those with pollinated stigmas. Finally, damaging the stigmas of flowers reduced ovipositions, although neither anther nor petal damage did so.

Conclusion: Host-marking signals and the cues of pollinated stigmas and of florivory aid in the differential exploitation of floral resources by senita moths and their uniform distribution of eggs among flowers.

Keywords: cue, florivory, oviposition, pheromone, signal.

INTRODUCTION

The quantity and quality of food resources exploited by consumers can play important roles in their abundance, distribution, and differential exploitation of resources. Although now extended to a variety of biological phenomena, some of the best documented cases

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involve an ideal free distribution, in which individual consumers distribute themselves among resources (or resource patches) in such a way that resource acquisition, and thus intraspecific competition, is similar among individuals exploiting the resource (Fretwell and Lucas, 1970; Fretwell, 1972). Influences of resources on the distribution of consumers can be particularly pronounced in insects that use small discrete food units as oviposition sites (e.g. flowers, immature fruits, and other insects), from which their larvae then grow and develop but do not disperse. For example, parasitoids are known to be selective in their choice of hosts, and their distribution and clutch size of eggs among hosts, which in turn can have later consequences for spatio-temporal dynamics of host–parasitoid interactions (Godfray, 1994; Hassell, 2000; Hochberg and Ives, 2000). Moreover, intraspecific competition among immobile larvae exploiting such small discrete food resources can reduce the number and size of larvae reaching maturity, and thereby the reproductive success of adults (Messina, 1991; Nagelkerke *et al.*, 1996; Sweeney and Quiring, 1998; Dukas *et al.*, 2001). In this way, ovipositing adults can influence their reproductive success through the selection and distribution of ovipositions among resources (Godfray, 1994; Price and Ohgushi, 1995; McClure *et al.*, 1998; Sweeney and Quiring, 1998).

Ovipositing insects may attain such selectivity through cues and signals that indicate the differential quality of resources for oviposition (Fox *et al.*, 1996; McClure *et al.*, 1998; Sweeney and Quiring, 1998; Allen and Hunt, 2001). In contrast to signals, cues convey such information only as an incidental by-product of a behaviour that has some alternative function (Nufio and Papaj, 2001). For example, oviposition scars made by yucca moths in yucca flowers may be a cue used by conspecifics to avoid oviposition and potentially strong intraspecific larval competition within developing fruits (Huth and Pellmyr, 1999). Signals, on the other hand, have the intended function of conveying information from a sender to a receiver, common examples being host-marking and oviposition-deterring pheromones (Nufio and Papaj, 2001). Such pheromones are often used by insects with low larval mobility, and whose hosts provide small discrete food resources, from which larvae grow and develop (Roitberg and Prokopy, 1987). These pheromones function to inhibit further ovipositions by conspecifics of previously exploited resources, thereby reducing intraspecific larval competition (Quiring *et al.*, 1998; Huth and Pellmyr, 1999; Nufio and Papaj, 2004). To further avoid low-quality resources that result in less successful offspring, ovipositing adults may also use cues arising from intra- or interspecific use of the food resource, such as herbivore-induced plant volatiles or florivore damage (Fatouros *et al.*, 2005; McCall and Irwin, 2006). Cues and signals may help insects to locate suitable oviposition sites not previously exploited and that are of sufficient quality to rear offspring (Huth and Pellmyr, 1999; Nufio and Papaj, 2004).

In this study, we examined signals and cues that may be utilized by senita moths in their exploitation of floral resources of senita cacti as oviposition sites, larvae of which then grow and develop within immature fruits from which they do not disperse (Holland and Fleming, 1999). As described in detail below, before oviposition on a flower, senita moths actively pollinate flowers by rubbing their pollen-covered abdomens directly onto stigmas, thereby ensuring pollination and increasing the likelihood of fruit set and the survival of eggs laid in flowers. Fruits developing from flowers on which eggs were laid serve as the sole food resource for larvae. Previous study of senita has shown that the oviposition of eggs by senita moths occurs in a non-random, uniform distribution among floral resources, in which many more flowers have one egg than expected by chance, and fewer flowers have zero, two, three, or more eggs than expected by chance (Holland and Fleming, 1999; Holland *et al.*, 2004a). Female moths appear to reduce intraspecific larval competition by laying only one egg per flower and by deterring conspecifics from further use of a previously exploited flower. A variety of signals and cues may be used by female moths to avoid intraspecific larval competition and low-quality floral resources. Specifically, we examined whether moths employed a host-marking or oviposition-deterring pheromone as a signal to reduce subsequent ovipositions in flowers by conspecifics. We also examined whether pollinated stigmas of flowers served as a cue for conspecifics subsequently visiting flowers, and whether florivore damage to stigmas, anthers, and petals was a cue for reduced quality of flowers as oviposition sites.

MATERIALS AND METHODS

Study system and study sites

Mutualistic interactions between senita cacti (*Pachycereus schottii*, Cactaceae) and pollinating seed-eating senita moths (*Upiga virescens* Hulst, Pyralidae) parallel in many ways the ecology and evolution of interactions between yucca and yucca moths (Fleming and Holland, 1998; Pellmyr *et al.*, 1996; Pellmyr, 2003). We studied interactions between senita cacti and senita moths in naturally occurring populations at Organ Pipe Cactus National Monument in south-central Arizona, USA (31°N, 112°W) and Bahia de Kino, Sonora, Mexico (28°N, 111°W) during the 2006 and 2007 flowering seasons. Senita is a multi-stemmed columnar cactus that attains heights of 2–4 m and lives for more than 75 years. Plants can produce thousands of buds and flowers from their areoles (spine-bearing pads) during the flowering season from April through July. Flowers are hermaphroditic, with an inferior ovary containing one pistil and hundreds of ovules and hundreds of anthers. Only 50% of flowers produce any nectar at all, with an average of ~0.5 μl in those nectar-producing flowers. Flowers open at sunset and often close before sunrise, thereby excluding diurnal co-pollinators. Due to resource limitation, only about 50% of flowers initiate fruit development, such that low fruit-to-flower ratios and fruit set (fraction of flowers initiating fruit maturation) result from trade-offs in resource allocation between flower production and fruit set, although pollen limitation has occurred in a few rare cases (Holland, 2002; Holland *et al.*, 2004b). Fruit abortion occurs within 6 days of anthesis and fruit mature within the following 30 days. Some immature fruit do not survive 20–25 days of fruit maturation (Holland, 2002; Holland *et al.*, 2004b), as some are destroyed by senita moth larvae (~21%) and other herbivores (Fleming and Holland, 1998; Holland and Fleming, 1999). Mature fruits are berry-like, with approximately 180 seeds per fruit.

Senita cacti rely almost exclusively on nocturnal senita moths for pollination and plant reproduction, as senita is self-incompatible and diurnal co-pollinating bees are rarely important (Holland and Fleming, 2002). Effective pollination is facilitated by the directed behavioural placement of pollen on stigmas by female moths (i.e. active pollination), and by the specialized morphological structure of elongated scales on the underside of their abdomens, which aid in pollen collection and transport among plants (Fleming and Holland, 1998; Holland and Fleming, 1999). Male moths do not pollinate. Female moths actively pollinate flowers by rubbing their pollen-covered abdomens directly onto stigmas. Following active pollination, moths oviposit a single egg within the open flower and onto the corolla, anthers or petals (Holland *et al.*, 2004a), and collect pollen by rubbing their abdomens among anthers (Holland and Fleming, 1999). Moth eggs are distributed uniformly among flowers, but not all eggs survive to produce a larva (Holland and Fleming, 1999; Holland *et al.*, 2004a). Eggs usually hatch after flowers close, larvae of which crawl down wilting corollas and bore into the developing ovary of the fruit. There, a larva consumes developing seeds and the immature fruit until both the fruit and larva are 9–16 days old, at which time the larva then exits the base of the fruit and bores into the cactus stem where it pupates (Holland and Fleming, 1999). All seeds in a fruit occupied by a larva are destroyed, as larval exit holes at the base of the fruit at the point of attachment to the areole cause fruit abscission before seed maturation. Pollination by senita moths leads to many more fruits than their larvae destroy, as not all pollinated flowers are oviposited, not all eggs hatch, and not all larvae survive to bore into or out of the fruit. Fruit abortion may function to limit moth population sizes and hence the oviposition rates of flowers (Holland and DeAngelis, 2002, 2006).

Host-marking pheromone and pollination experiments

We examined whether female senita moths produced a biochemical (e.g. a pheromone) to deter flower visitation and oviposition by subsequent conspecific female moths that may approach a previously visited flower. Employing methods used to examine a host-marking pheromone in yucca moths (Huth and Pellmyr, 1999), we created a moth abdomen homogenate by finely grinding individual female moth abdomens using a mortar and pestle, and then diluting each with ~60 μl of distilled water. We used water in accord with Huth and Pellmyr (1999), as we had no *a priori* reason to evaluate the solubility of a potential pheromone and as the purpose of the water was to make an aqueous solution for application to flowers. Adult female moths were randomly collected among individuals within a natural moth population. This homogenate extract was then used in an experiment to test for differential use of control and pheromone-extract-treated flowers by female moths. Each abdomen extract was used only once for only one flower. The pheromone-extract treatment was set up by applying ~20 μl of the extract to the lower half of petals with a small paintbrush (see below for water-addition experiment that tested for potential unrecognized effects of such flower manipulations). We conducted six trials of this experiment, with sample sizes ranging from 9 to 14 plants and from 80 to 142 flowers per trial, for a total of 644 flowers among trials. Within each plant, study flowers were divided equally between control and pheromone-treated flowers. All study flowers were labelled and treated at sunset and before moth activity. Then, about 3 h later after moth activity, we scored moth responses to the flowers. We scored flowers based on their pollination and oviposition status ('no', 'yes'), both of which unambiguously reflect female moth visitation to flowers. Pollination status was readily assessed by carefully inspecting stigmas for pollen deposition with a 10× hand lens. Oviposition status was also easily assessed by visual inspection of flowers for eggs. Flowers that contained herbivores or showed signs of herbivory at the time of their assessment were removed from the study, as such florivory may also affect pollination and moth use of floral resources (see below) (McCall and Irwin, 2006).

In addition to, or possibly as an alternative to, a host-marking pheromone, female moths may avoid previously exploited flowers based on the cue of the pollination status of the flower's stigma. Using similar protocols as those described above, we conducted an experiment to test the effect of a pollinated stigma on moth use of the floral resource. We conducted four trials in which we divided flowers within a plant equally among control and hand-pollination treatments. The hand-pollination treatment consisted of applying the anthers of half of one fresh flower from another individual plant to the stigma of the focal treatment flower (Holland and Fleming, 1999, 2002; Holland, 2002). As described above, flowers were censused for their oviposition status. Sample sizes ranged from 6 to 10 plants and from 55 to 93 flowers per trial, for a total of 319 flowers among trials.

Due to time constraints associated with applying treatments in the short period between flower opening and the onset of moth activity, we were unable to include a third water-addition treatment to test for any unintended treatment effects of flower manipulations in the pheromone experiment. An analysis of such potential treatment effects is important, as moths could simply avoid treated flowers due to some unrecognized influence arising from their manipulations. We conducted an additional experiment examining differences in moth use of control unmanipulated flowers and a water-addition treatment, which differed from the pheromone treatment only in applying water rather than an abdomen extract. We conducted four trials of this experiment using the above-described protocols and moth responses of pollination and oviposition. Sample sizes ranged from 7 to 12 plants and from 55 to 136 flowers per trial, for a total of 402 flowers among trials.

Chi-square tests of heterogeneity among trials for each of the pheromone, water-addition, and pollination experiments indicated that the data among individual trials were not significantly heterogeneous (Zar, 1999). For this reason, we were able to combine data among individual trials within each experiment. We tested for differences in pollination and oviposition status between control and treatment flowers using Fisher's exact test (Zar, 1999). For the pheromone study, we used a one-tailed Fisher's exact test with the prediction that pollination and oviposition rates would be higher for control than for pheromone-treated flowers. For the pollination experiment, we used a one-tailed Fisher's exact test with the prediction that oviposition rates would be higher for control flowers than for pollinated flowers. We used one-tailed tests based on *a priori* predictions derived from the empirical uniform egg distribution among flowers. For the water-addition experiment, we used a two-tailed Fisher's exact test with no explicit *a priori* prediction for pollination and oviposition rates between control and treatment flowers.

Florivory experiment

In addition to potential intraspecific influences of a host-marking signal and a pollination cue, interspecific interactions between senita cactus flowers and florivores may influence senita moth exploitation of floral resources. Any potential response of moths to florivory may vary with the particular floral parts consumed, including stigmas, anthers, and petals. Florivores of senita do indeed consume different floral parts. For example, crickets routinely limit their consumption of flowers to anthers, whereas longhorn beetles are much less selective, consuming any portion of flowers. To examine moth responses to physical flower cues caused by florivore damage, we conducted an experiment with control flowers and three florivore damage treatments: (1) stigma clipping, in which the entire stigma and large portion of the style were removed from flowers; (2) anther clipping, in which about a third of all anthers were removed mostly from the bottom half of flowers (where pollen collection typically occurs); and (3) petal clipping, in which about a quarter of all petals were removed mostly from the bottom half of the flowers. Within each plant, focal flowers of study were distributed equally among control and florivory treatments. We conducted eight trials of this experiment using the above-described protocols and moth responses of pollination (not in the stigma clipping analysis) and oviposition. Sample sizes ranged from 6 to 14 plants and from 60 to 124 flowers per trial, for a total of 589 flowers among trials. Chi-square tests of heterogeneity among the trials indicated that data among individual trials were not significantly heterogeneous (Zar, 1999). We analysed these

Table 1. Use of floral resources by female senita moths, as measured by their pollination and oviposition responses, to control and treated flowers, for three experiments involving treatments of water addition, pheromone extract, and hand-pollinated stigmas

		Control		Treatment		
Treatment	Response	No	Yes	No	Yes	*P*-value
Water	Pollination	167	40	161	34	0.3600
	Oviposition	184	23	178	17	0.2634
Pheromone	Pollination	276	50	287	31	0.0214
	Oviposition	288	36	294	24	0.0782
Pollination	Oviposition	50	86	74	59	0.0022

Note: Values for 'No' and 'Yes' represent the number of flowers for which pollination or oviposition occurred for each of the control and treatment flowers for each of the three experiments. *P*-values are for one-tailed Fisher's exact tests for pheromone and pollination experiments and two-tailed Fisher's exact tests for the water-addition experiment.

data using Pearson chi-square statistics. When the overall Pearson chi-square test was significant, we used 95% confidence intervals of odds ratios to compare differences among treatments.

RESULTS

Neither pollination nor oviposition by female moths differed significantly between control, unmanipulated, and water-addition treatment flowers (Table 1), indicating that moth responses to treatments were not confounded by artificial manipulations of treatment flowers. Pollination was significantly lower, and oviposition marginally significantly lower, for flowers treated with the moth abdomen homogenate than control flowers (Table 1). Of the pheromone-treated flowers, 9.7% and 7.5% were pollinated and oviposited, respectively, compared with 15.3% and 11.1% pollination and oviposition for control flowers. No flower in either the water-addition or pheromone experiment received more than one oviposition. These results suggest that females may use a host-marking or oviposition-deterring pheromone to reduce the likelihood of subsequent use of a floral resource by conspecifics. Oviposition was also significantly lower for hand-pollinated than control flowers (Table 1). Of the hand-pollinated flowers, 44.4% were oviposited, whereas 63.2% of control flowers were oviposited. These results suggest that, in addition to a potential host-marking and oviposition-deterring pheromone, pollinated stigmas may also be a cue used by female moths to avoid previously exploited floral resources. The differences in percent oviposition between the experiments can be attributed to differences in moth abundance at the different times that the experiments were conducted.

Florivory did have some consequences for moth exploitation of floral resources, although its effects were less pronounced for pollination than oviposition. There was a nearly significant effect of florivory on the pollination status of flowers (Table 2). Of the control, anther, and petal treatment flowers, 22.7%, 13.5%, and 20.7% were pollinated, respectively, with a trend for fewer pollinations for flowers with anther damage. On the other hand, there

Table 2. Discrimination among floral resources by female senita moths, as measured by their pollination and oviposition responses to florivory

	Treatment									
	Control		Stigma		Anthers		Petals			
Response	No	Yes	No	Yes	No	Yes	No	Yes	χ^2	*P*-value
Pollination	122	36	–	–	134	21	122	32	4.769	0.0922
Oviposition	127	22	146	1	137	10	130	16	21.141	<0.0001

Note: Florivory treatments included control, undamaged flowers, and artificial damage to stigmas, anthers, and petals. Values for 'No' and 'Yes' represent the number of flowers for which pollination or oviposition occurred. The Pearson chi-square and associated *P*-values are reported (α = 0.05) for each of pollination and oviposition.

was a strong significant effect of florivory on oviposition status of flowers (Table 2). Of the control, stigma, anther, and petal treatments, 14.7%, 0.7%, 6.8%, and 10.9% were oviposited, showing a strong pattern of fewer ovipositions on flowers in which stigmas were consumed. Indeed, significantly fewer ovipositions (based on 95% CI of odds ratios) occurred on the stigma treatment than each of control, anther, and petal treatments. Similarly, there were fewer eggs laid on anther treatment flowers than controls, while all other pairwise comparisons were not significant.

DISCUSSION

When larvae are relatively immobile and rely upon small discrete units of food such as flowers and immature fruits, ovipositing adults may increase their reproductive success by selectively avoiding those resource units of low quality and low likelihood to nourish their offspring. Such influences of flower and fruit resources on the oviposition behaviour of insects are particularly evident in specialized insects that exploit one or a very few host species, including yucca–yucca moth, senita–senita moth, and fig–fig wasp interactions, in which adults actively pollinate and oviposit the flowers that they exploit (Pellmyr *et al.*, 1996; Holland and Fleming, 1999; Weiblen, 2002; Pellmyr, 2003). In the senita cactus–moth system, larvae have relatively high survival rates (~20%), as many eggs produce larvae that reach adulthood (Holland and Fleming, 1999). Such reproductive success of senita moths arises, at least in part, from the uniform distribution of eggs among floral resources (one egg per flower) (Holland and Fleming, 1999; Holland *et al.*, 2004a), which may well minimize intraspecific larval competition. The present results suggest that female moths utilize signals and cues in their selective avoidance and uniform exploitation of floral resources as oviposition sites.

Laying only one egg per flower and avoiding oviposition sites previously exploited by conspecifics can indeed curtail intraspecific larval competition. Ovipositions were greater for control flowers than for moth abdomen-treated flowers, suggesting that females produce a chemical that functions to deter subsequent exploitation of flowers by conspecifics. This result of selectively avoiding abdomen-treated flowers is not simply an artefact of manipulating flowers, as pollination and oviposition did not differ between control unmanipulated and water-treated flowers. Moreover, if we assume that oviposition on an abdomen-treated flower is analogous to a flower receiving two ovipositions, then only 3.7%

of oviposited flowers in the present study received a second oviposition. This low percentage of two ovipositions on a flower is consistent with and statistically insignificant from the 2.5% of flowers that received two eggs in a study of natural egg distributions (Fisher's two-tailed exact test, $P = 0.255$) (Holland *et al.*, 2004a). Similar natural oviposition rates here and in previous research further suggests that the abdomen-extract treatment was largely effective in representing natural conditions.

Although not definitively identified as such, our results are consistent with the presence of a signalling pheromone, such as a host-marking or oviposition-deterring pheromone. To this end, a moth's behaviour during flower visitation often entails dragging its abdomen along the surface of the petals, which may be host-marking behaviour. The deposition and avoidance of a host-marking pheromone may contribute to the uniform distribution of eggs among floral resources. For several reasons, however, there is at best only weak support for this conclusion of a signalling pheromone. First, we have not explicitly identified or isolated any such compound and tested it directly. Second, we did not include a separate control for the moth-abdomen homogenate, such as a moth-abdomen homogenate of another insect or moth species. And third, egg chemistry or some other factor may affect moth avoidance of flowers, and we were unable to isolate it from the moth-abdomen homogenate. This last shortcoming, if true, would nevertheless support our speculation that some moth-based cue contributes to the uniform egg distribution that reduces intraspecific larval competition.

In addition to the signal of a host-marking pheromone, female moths also used pollinated stigmas as a cue to selectively avoid a floral resource. In senita, yucca, and many fig systems, so-called active pollination by female insects involves the deliberate, directed placement of pollen on stigmas (Pellmyr *et al.*, 1996). In the case of senita moths, immediately upon arrival to a flower, females rub their pollen-covered abdomens directly onto stigmas and then subsequently oviposit (Holland and Fleming, 1999). Such behavioural adaptations for interacting with flowers presumably evolved to ensure pollination and thereby increase the likelihood of fruit resources for the growth, development, and survival of larvae hatching from eggs oviposited (Pellmyr *et al.*, 1996). Even though a pollinated stigma is a novel cue for selective avoidance of a flower by an ovipositing insect, it is not surprising given how tightly coupled pollination and oviposition are in the ecology and evolution of senita moths. In the yucca system, moths selectively avoid or reduce their exploitation of flowers with many prior ovipositions, presumably from some cue associated with ovipositor damage to flowers (Wilson and Addicott, 1998; Huth and Pellmyr, 1999). Senita moths may avoid flowers based on the visual cue of an egg, although such an experiment would need to remove any possible oviposition-deterring pheromone (located on the egg itself) to assess eggs as a visual cue. While eggs laid within the corolla tube or anthers have about 40% higher survival to pupation than eggs laid on petals, most eggs (~80%) are laid on petals (Holland *et al.*, 2004a). Such placement of eggs on petals may have the advantage of being a cue that further deters subsequent oviposition.

As the survival of eggs oviposited on flowers by female moths is entirely contingent upon the flower setting fruit, florivory may reduce the reproductive success of ovipositing moths by inducing flower abscission and the mortality of larvae therein. For this reason, ovipositing moths may use cues of florivore damage to selectively avoid such low-quality floral resources. Although not as strong as the host-marking signal or the pollinated stigma cue, florivore damage did serve to some degree as a cue for female moths in selectively avoiding floral resources. Specifically, florivore damage to anthers and petals did not have a strong effect on pollination compared with controls, but florivore damage of stigmas did reduce ovipositions compared with controls and anther and petal damage. Only in one of 147 flowers did a female oviposit on a flower with a clipped stigma. There was also some indication that oviposition was reduced due to anther damage. Selective avoidance of flowers based on stigma damage, or in this case its complete consumption, is consistent with female moths using pollinated stigmas as a cue. A stigma is the first point of interaction between female moths and flowers, so it is not surprising that moths avoided flowers that lacked a stigma. Clearly, flowers for which stigmas have been consumed by florivores will not set fruit and provide larvae with nourishment.

Having shown that signals and cues contribute to selective avoidance of floral resources, we briefly discuss some ecological conditions in the senita system that may be of particular importance in the development of flower avoidance by moths and uniform exploitation of floral resources. First, due to resource limitation, only about 50% of pollinated flowers set fruit, leading other flowers to abort and not initiate fruit development (Holland, 2002; Holland *et al.*, 2004b). Unlike the yucca system (Pellmyr and Huth, 1994), fruit abortion in the senita system is not selective, but random (Holland *et al.*, 2004b). All pollinated and oviposited flowers have an equal chance of setting fruit or being aborted, regardless of egg load. Female moths may minimize mortality risks of fruit abortion to their offspring by distributing their eggs uniformly among flowers (one egg per flower), rather than ovipositing two or more eggs within a single flower. Any cues or signals that aid a female moth in recognizing flowers she previously exploited may minimize the effects of fruit abortion on pre-adult mortality. Nonetheless, fruit abortion alone may not account for the flower avoidance, as there are no apparent consequences for moths exploiting a previously oviposited flower.

Second, each individual fruit represents a small, limited unit of food resources from which a larva may grow and develop. A maturing fruit appears to support only one larva, as each larva typically consumes upwards of 75% of ovules within a fruit. Larvae do not appear to be able to disperse among fruit. Thus, multiple ovipositions on a flower by either a single female or several conspecifics may result in intraspecific competition, leading to stunted development and smaller larval sizes due to exploitative competition, or death due to scramble competition or cannibalism. Unlike systems in which larvae of earlier ovipositions may have a developmental and competitive advantage over later ones (Quiring and McNeil, 1984), moth oviposition occurs within less than 3 h of the relatively short time period (< 12 h) in which flowers are available for oviposition. Distinct chronological sequences of ovipositions in which developmental and competitive advantages may arise are not likely to occur in the senita system. Although not mutually exclusive of fruit abortion, the consequences of such finite fruit resources for the offspring of moths may also contribute to why moths selectively avoid particular flowers through the use of signals and cues indicative of prior ovipositions.

While interactions between senita cacti and senita moths do form a mutualism, the interaction is in its most basic form a consumer–resource interaction in which moths pollinate flowers in the process of exploiting floral resources as oviposition sites. The uniform distribution of moth eggs among floral resources represents an ideal free distribution, in which moths exploit and distribute their eggs among floral resources in such a way as to avoid larval competition, such that resource acquisition is similar among individuals. To this end, our work has shown several means by which moths may attain such an ideal free distribution, namely through the recognition of host-marking signals and other cues that indicate a less than ideal scenario for intraspecific competition. While this study is an important step in identifying how such an ideal free distribution arises, further studies are needed which manipulate egg number per fruit, larval competition, and fruit abortion to distinguish among possible reasons for the uniform distribution of eggs and the use of signals and cues by senita moths. Detailed analyses of sequential moth behaviours during flower visitation, including active pollination and oviposition behaviours, will yield further insights into the evolutionary ecology of flower visitation behaviours that facilitate female reproductive success and reduce intraspecific competition.

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