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Oviposition choice and larval survival of an obligately pollinating granivorous moth

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ABSTRACT

Animal species not investing in parental care can nevertheless influence the success of their progeny by actively selecting sites that are most favourable for their growth and survival. Primarily through the study of phytophagous insects, it has become clear that oviposition behaviour, and choice of oviposition sites in particular, can increase the performance and survival of insect progeny. Such oviposition behaviour is largely driven by variation in the environment. In this study, we examined oviposition choice and larval survival of the senita moth (*Upiga virescens*), which is an obligately pollinating granivore of a single host plant, the senita cactus (*Lophocereus schottii*). Although senita moths oviposit only on open flowers of senita cacti, eggs are laid among four relatively discrete sites on flowers: between or underneath petals, on the outward-facing side of petals, on anthers and within the corolla tube. In a population of senita cacti in southern Arizona, we quantified the distribution of eggs among flowers and plants, the distribution of eggs among oviposition sites, and larval (egg-to-pupa) survival among oviposition sites. Eggs were evenly distributed among flowers, but plants with more flowers had greater numbers of eggs than plants with few flowers. On the other hand, eggs were unevenly distributed among oviposition sites within flowers. Eggs were most frequently laid on petals, and least frequently laid on anthers and corolla tubes. Inconsistent with this result, larval survival was greater for anthers and corolla tubes than for petals. However, taking into account differences in surface area among oviposition sites, anthers and corolla tubes received disproportionately greater numbers of eggs than expected by chance, while petals received slightly fewer eggs than expected given surface area. This result is consistent with larval survival being greater for anthers and corolla tubes. We discuss potential ecological and evolutionary reasons for why selection has apparently favoured an even distribution of eggs among flowers, but has not more strongly favoured ovipositing into corolla tubes and anthers where progeny survival is greatest.

Keywords: behaviour, egg, fruit abortion, larva, mutualism, oviposition, senita, survival.

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INTRODUCTION

Determinants of oviposition choice by phytophagous insects include allelochemicals, quantity and/or quality of resources, plant morphology and natural enemies (Thompson and Pellmyr, 1991). Such factors can lead to variation in performance and survival of insect progeny for eggs deposited in different locations (Rausher, 1979; Simberloff and Stiling, 1987; Craig *et al.*, 1989; Resetarits, 1996; Mayhew, 1997; Stamps and Linit, 2002). Because variation in oviposition behaviour can be genetic and heritable (Jaenike, 1990; Jaenike and Holt, 1991; Thompson and Pellmyr, 1991), natural selection may favour the choice of oviposition sites that facilitate growth and survival of offspring.

Choice of oviposition sites and dispersion of eggs by adult insects can vary among host species, among individuals within a host population, and within an individual of a particular host population. A positive correlation between oviposition choice and offspring performance may be expected for specialized interactions in which an insect relies entirely on one host species, particularly co-evolved insect–plant interactions. Interactions involving both pollination and granivory by insects, such as yucca/yucca moth, fig/fig wasp and globeflowers/*Chiastocheta* flies, represent cases of presumable co-evolution in which the insect species is usually obligately host specific. These interactions involve adult insects that pollinate flowers of host plants, but also oviposit into the flowers. Larvae rely upon food resources of the developing fruit. Larvae do not move among flowers and fruit, but instead remain on the flower/fruit food resource on which their mother oviposited. Even though these insects oviposit only on flowers of one host species, variation may occur in how adult insects distribute their eggs among flowers and plants within the host population, as well as in the exact placement of eggs within flowers. Such variation may lead to differential survival of offspring. Given that these species-specific systems are so intimate and that they probably co-evolved, they may provide particularly useful tests of the general idea that oviposition choice and offspring performance should be positively correlated.

In this study, we examined the oviposition behaviour and larval survival of senita moths, which are obligately involved in a pollinating seed-consuming interaction with senita cacti (Holland and Fleming, 1999). Even though senita moths oviposit only on flowers of senita cacti, the heterogeneous structure of open flowers provides different sites for moth oviposition choice, including petals, anthers and corolla tubes. We addressed four primary questions concerning senita moth oviposition behaviour: (1) Do senita moths distribute their eggs in a clumped, uniform or random fashion among flowers within a senita cactus population? (2) Does egg distribution among plants vary with flowers per plant? (3) Do moths differentially distribute their eggs among oviposition sites within flowers (petals, anthers and corolla tubes)? (4) Does larval survival vary among oviposition sites within flowers? We discuss our results in terms of ecological and evolutionary factors that may influence senita moth oviposition behaviour.

MATERIALS AND METHODS

Study site and study species

We studied senita moth (*Upiga virescens*; Pyralidae) and senita cactus (*Lophocereus schottii*) interactions at Organ Pipe Cactus National Monument (OPCNM), Pima County, Arizona, USA (31°57′N, 112°52′W) from April to August 2002. Both senita moths and senita cacti are endemic to the Sonoran Desert of northwestern Mexico and OPCNM. Senita cacti are self-incompatible and hermaphroditic; nightly production of small whitish-pink flowers occurs from April to August. Senita moths use only senita cacti as a host plant. The moths are small, swift fliers that are difficult to follow among flowers and plants. They oviposit only on open flowers of senita cacti. The moths do not pierce plant tissue, but instead lay their eggs on the plant tissue of flowers. Larvae hatching from eggs rely on developing fruit for food. Flowers remain open for only one night, such that each individual flower is available for oviposition for only one night. Within a few days after flower closing, larvae move through wilting petals and down the corolla tube to bore into the immature fruit. They then consume developing seeds and fruit tissue before entering the cactus stem to pupate. Not all pollinated flowers receive an egg and not all larvae survive to consume fruit. Due to limited resources for fruit maturation, not all pollinated flowers set fruit, such that larvae in aborted fruit die. Further details on senita cacti, senita moths and their interactions can be found elsewhere (Holland and Fleming, 1999; Holland, 2003).

Distribution of eggs among flowers and plants

One aspect of insect oviposition behaviour is how eggs are distributed among resources. Although senita moths invariably lay their eggs only in flowers of senita cacti, they may distribute their eggs among flowers in a random, uniform (even) or clumped fashion. Furthermore, if flowers are not evenly distributed among plants, then moths may distribute their eggs differently among individual cacti within the plant population. We assessed how senita moths distribute their eggs among flowers by inspecting for eggs in 596 flowers across 22 plants over five nights. We recorded the number of eggs observed per flower. Using a chi-squared test, we assessed whether eggs were distributed in a clumped, random or uniform fashion by comparing the observed distribution of eggs among flowers with that expected based on a Poisson distribution (Zar, 1999). We also examined how egg number per plant varied with flower number per plant. Due to heteroscedasticity and non-linearity, the among-plant data were log-transformed and then analysed using linear regression.

Distribution of eggs among oviposition sites within flowers

Even though senita moths lay their eggs only in flowers of senita cacti, anecdotal observations indicated that their oviposition behaviour varies in the exact placement of eggs within the heterogeneous structure of flowers. We identified four relatively discrete areas within flowers in which eggs may be laid (Fig. 1): ‘petals A’, between or underneath petals; ‘petals B’, on the outward-facing surface of petals; ‘anthers’, among the anthers; and ‘corolla tube’, below the anthers within the corolla tube. On seven nights during the flowering season we inspected 804 flowers among 26 plants. For each of the 522 eggs observed, we recorded in which of the four oviposition sites the egg was located. Using a chi-squared test, we assessed for heterogeneity in egg data among the seven nights. We used chi-squared tests to assess if differences occurred in the number of eggs laid among the four demarcated oviposition sites. We performed this test for all flowers censused, for only flowers containing one egg, for only flowers containing two eggs, for only flowers containing three eggs, and for only flowers containing four eggs. Of the 804 flowers censused, only five flowers had more than four eggs per flower. Because of such low sample sizes, chi-squared tests were not

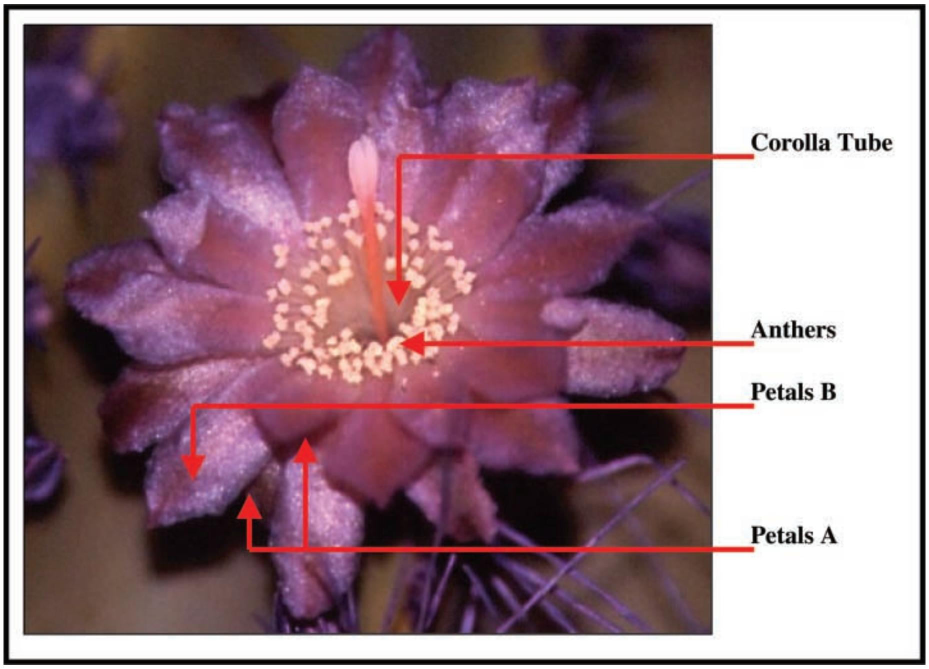

Fig. 1. A flower of the senita cactus (*Lophocereus schottii*) showing each of four relatively discrete senita moth oviposition sites. The 'Petals A' site is between or underneath petals, the 'Petals B' site is on the outward-facing surface of petals, the 'Anthers' site is among anthers, and the 'Corolla tube' site is within the corolla tube below the anthers.

performed for only flowers with five eggs. Furthermore, caution should be taken when interpreting statistics for three and four eggs per flower due to small sample sizes.

We also examined egg distribution among oviposition sites while accounting for differences in surface area among the four oviposition sites. Surface area of each oviposition site was calculated using previously collected morphological data for flowers (Holland and Fleming, 1999). The surface area of oviposition sites 'petals A' and 'petals B' were assumed to be similar. This surface area was calculated based on the area of a circle, $A = \pi r^2$, where A is the area of the circle, π is pi and r is the radius of the circle. The area of the mouth of the corolla tube was deducted from the measure of petal surface area as this is the open area of flowers not containing petal surface. The surface area of the anthers was calculated based on the area of a cylinder ($A = 2\pi rh$, where h is the right angular height of the cylinder) because anthers form a cylindrical shape near the mouth of the corolla tube. The surface area of the corolla tube was estimated based on a conical frustrum:

$$A = \pi(r_1 + r_2)s = \pi(r_1 + r_2)\sqrt{(r_1 - r_2)^2 + h^2}$$

where r_1 is the radius of the larger circle of the conical frustrum (top of corolla tube), r_2 is the radius of the smaller circle of the conical frustrum (bottom of corolla tube), s is the slant height (slant of corolla tube), and h is right angular height of the frustrum (height of corolla tube). We performed chi-squared tests to assess differences in egg numbers among the four oviposition sites. To account for differences in surface area among oviposition sites, observed egg numbers for each oviposition site were compared with expected numbers given the proportional representation of total oviposition area for a given oviposition site.

Larval survival among oviposition sites

To assess if larval (egg-to-pupa) survival varied among the four oviposition sites, we followed the fate of 407 eggs occurring singly in flowers. Each of the 407 flowers was labelled and the oviposition site recorded (Fig. 1). Each labelled flower was censused daily until the fruit either abscised from the plant or ripened. During days 8–16 after flower closing, each surviving larva necessarily results in the abscission of the immature fruit it occupied. This is because the surviving larva invariably exits the immature fruit by boring a hole into the cactus stem at the point where the immature fruit is attached to the cactus (Holland and Fleming, 1999; Holland, 2003). Larval survival among the four oviposition sites was evaluated based on differences in the proportion of labelled flowers abscising from cacti. However, during days 1–6 after flower closing, but no later, some fruit abort and fall off cacti, not because of larvae, but due to limited plant resources available for fruit maturation (Holland, 2002; Holland *et al.*, in press). Fruit abortions due to this resource limitation during days 1–6 result in the death of eggs and early instar larvae within them (Holland and Fleming, 1999). Thus, both oviposition site and resource-limited fruit set may influence larval survival. Using chi-squared tests for comparing multiple proportions (Zar, 1999), we first analysed for differences in resource-limited fruit set among the four oviposition sites to assess whether oviposition site influenced fruit set and to ensure that data for fruit abscission due to larvae was not biased by unequal fruit set among oviposition sites. We then analysed for differences in survival among the four oviposition sites. We examined which oviposition sites differed from one another in egg-to-pupa survival with chi-squared tests for comparing multiple proportions (Zar, 1999). Proportions were not arcsine transformed due to large sample sizes.

RESULTS

Distribution of eggs among flowers and plants

Of the 596 flowers we censused for eggs, 57.7, 39.4, 2.5 and 0.4% had zero, one, two and three eggs, respectively. Based on a random Poisson distribution of eggs among flowers, 63.4, 28.9, 6.5 and 1% of flowers were expected to have zero, one, two and three eggs, respectively. Significantly fewer flowers had zero eggs than expected, more flowers had one egg than expected, and fewer flowers had greater than one egg than expected ($\chi^2 = 43.6$, d.f. = 2, $P < 0.0001$). The σ^2/μ ratio was 0.248. Senita moths do not distribute their eggs in either a random or clumped fashion among flowers; rather, they lay their eggs evenly among flowers, with flowers typically having one egg. Consistent with this even distribution of eggs among flowers was an uneven distribution of eggs among plants, given that plants produced different numbers of flowers (Fig. 2). Plants with greater numbers of flowers had greater numbers of eggs laid on their flowers ($F_{1,252} = 727$, $P < 0.0001$; Fig. 2).

Distribution of eggs among oviposition sites within flowers

Heterogeneity in the distribution of eggs did not occur among nights ($\chi^2 = 34.033$, d.f. = 2, $P < 0.001$). Of the 522 eggs for which oviposition site was recorded, 33.3% of eggs were

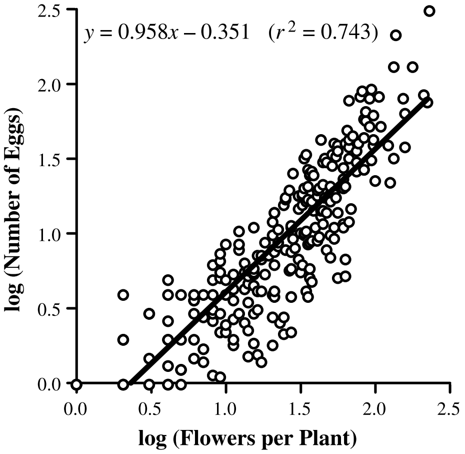

Fig. 2. Number of eggs laid by senita moths per senita cactus as a function of number of flowers produced per cactus.

located on 'petals A', 49.2% on 'petals B', 10.7% on anthers and 6.7% within corolla tubes (Table 1). The distribution of eggs among these four sites differed significantly from that expected by chance regardless of whether analyses were for all flowers with eggs, for only flowers with one egg, for only flowers with two eggs, and so forth for flowers with three and four eggs (Table 1). The above patterns in egg distribution remained when 'petals A' and 'petals B' sites were grouped as one oviposition site and when 'petals A' and 'petals B' were grouped and 'anthers' and 'corolla tubes' were grouped as oviposition sites (Table 1). In sum, senita moths oviposited most frequently on petals (83%) and least frequently in anthers and corolla tubes (17%).

Petals, anthers and corolla tubes represent different surface areas for oviposition within flowers. Each of 'petals A' and 'petals B' oviposition sites are on average 7.74 cm^2, anthers are 1.18 cm^2 and corolla tubes are 1.22 cm^2. Such differences in surface area may contribute to patterns of egg distribution among oviposition sites within flowers. We performed an additional set of analyses on egg distribution, accounting for differences in surface area among the oviposition sites (Table 2). As with analyses of frequency of eggs among oviposition sites, the distribution of eggs among the four oviposition sites, after taking into account differences in surface areas, differed significantly from that expected by chance (Table 2). However, in contrast to the analyses of egg frequency without accounting for surface area, when accounting for differences in surface area anthers and corolla tubes received disproportionately greater numbers of eggs than expected by chance and petals received slightly fewer eggs than expected given surface area.

Larval survival among oviposition sites

Fruit set did not vary significantly among the four oviposition sites ($\chi^2 = 2.847$, d.f. = 3, $P > 0.05$; Fig. 3A), indicating that where senita moths oviposit within flowers does not influence larval mortality resulting from fruit abortion. However, egg-to-pupa survival did vary among the four oviposition sites ($\chi^2 = 29.036$, d.f. = 3, $P < 0.001$; Fig. 3B). Survival did not vary between eggs laid on 'petals A' and 'petals B' (Fig. 3B), nor did survival vary

Table 1. Observed and expected number of senita moth eggs among oviposition sites within flowers of senita cacti for all flowers with eggs and those flowers for which there were one, two, three or four eggs

	Observed number of eggs				Expected number of eggs	χ^2	*P*
	Petals A	Petals B	Anthers	Corolla			
All eggs	174	257	56	35	130.50	249.5	<0.0001
1 egg/flower	143	180	53	35	102.75	142.6	<0.0001
2 eggs/flower	19	60	3	0	20.50	111.7	<0.0001
3 eggs/flower	6	6	0	0	3.0	12.0	<0.008
4 eggs/flower	4	8	0	0	3.0	14.7	<0.003
	Petals A & B		Anthers	Corolla			
All eggs	431		56	35	174	570.6	<0.0001
1 egg/flower	323		53	35	137	380.0	<0.0001
2 eggs/flower	79		3	0	27.3	146.7	<0.0001
3 eggs/flower	12		0	0	4	24	<0.0001
4 eggs/flower	12		0	0	4	24	<0.0001
	Petals A & B		Anthers & corolla				
All eggs	431		91		261	221.5	<0.0001
1 egg/flower	323		88		205.5	134.4	<0.0001
2 eggs/flower	79		3		41	70.4	<0.0001
3 eggs/flower	12		0		6	12	<0.003
4 eggs/flower	12		0		6	12	<0.003

Note: Figure 1 depicts the oviposition sites. Expected number of eggs is based on total number of eggs observed divided by the number of categories of oviposition sites.

between eggs laid on anthers and corolla tubes (Fig. 3B). Significant differences did occur in survival between eggs laid on petals and in eggs laid on anthers/corolla tubes (Fig. 3B). Eggs laid among anthers or within the corolla tube had ~40% higher survival to the pre-pupa life stage than eggs laid on petals.

DISCUSSION

In this study, we examined how oviposition behaviour and egg-to-pupa survival varied for an insect (senita moth) specialized on a single host plant (senita cactus). While senita moths oviposit only on open flowers of senita cacti, their oviposition behaviour determines the distribution of eggs among flowers and plants, as well as the exact placement of eggs within the heterogeneous structure of flowers, both of which may alter larval survival. We found that the oviposition behaviour of senita moths resulted in an even distribution of eggs among flowers within the cactus population, but an uneven distribution among plants, as plants varied in their production of flowers. More ovipositions occurred on plants with many, rather than few, flowers. This is not a surprising result, as it has long been recognized

Table 2. Observed (Obs.) and expected (Exp.) number of eggs among oviposition sites for all flowers with eggs and those flowers for which there were one, two, three or four eggs

	Petals A		Petals B		Anthers		Corolla			
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	χ^2	*P*
All eggs	174	226	257	226	56	34.5	35	35.6	29.7	<0.0001
1 egg/flower	143	178	180	178	53	27.1	35	28.0	33.3	<0.0001
2 eggs/flower	19	35	60	35	3	5.4	0	5.6	31.3	<0.0001
3 eggs/flower	6	5.2	6	5.2	0	0.8	0	0.8	1.9	<0.602
4 eggs/flower	4	5.2	8	5.2	0	0.8	0	0.8	3.4	<0.334

	Petals A & B		Anthers		Corolla			
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	χ^2	*P*
All eggs	431	451.9	56	34.5	35	35.6	14.5	<0.0001
1 egg/flower	323	355.8	53	27.1	35	28.0	29.4	<0.0001
2 eggs/flower	79	71.0	3	5.4	0	5.6	7.6	<0.023
3 eggs/flower	12	10.4	0	0.8	0	0.8	1.9	<0.400
4 eggs/flower	12	10.4	0	0.8	0	0.8	1.9	<0.400

	Petals A & B		Anthers & corolla			
	Obs.	Exp.	Obs.	Exp.	χ^2	*P*
All eggs	431	451.9	91	70.1	7.2	<0.008
1 egg/flower	323	355.8	88	55.2	22.6	<0.0001
2 eggs/flower	79	71.0	3	11.0	6.7	<0.01
3 eggs/flower	12	10.4	0	1.6	1.9	<0.20
4 eggs/flower	12	10.4	0	1.6	1.9	<0.20

Note: Expected number of eggs differs among oviposition sites given differences in their surface areas. Expected number of eggs was estimated based on proportion of total oviposition site area of a particular site.

that pollinator attraction and visitation to plants can vary with flower production (Willson and Rathcke, 1974; Willson and Price, 1977; Schaffer and Schaffer, 1979; Willson and Schemske, 1980).

We also found that senita moths distributed their eggs unevenly within flowers, with greater absolute numbers of eggs being laid on petals than in anthers or corolla tubes. This result does not support the often observed correlation between oviposition choice and larval performance, as egg-to-pupa survival of senita moths was greater for eggs laid in anthers and corolla tubes than for eggs laid on petals. However, when surface area of oviposition sites was taken into account, more eggs were laid in anthers and corolla tubes than on petals. This result is consistent with insect oviposition choice favouring larval performance. Correlations between oviposition preference and larval performance, including preferences for different sites within a plant (or, in this case, flower), range from good to poor among insects (Rausher, 1979; Karban and Courtney, 1987; Simberloff and Stiling, 1987; Thompson, 1988; Thompson and Pellmyr, 1991; Valladares and Lawton, 1991; Mayhew,

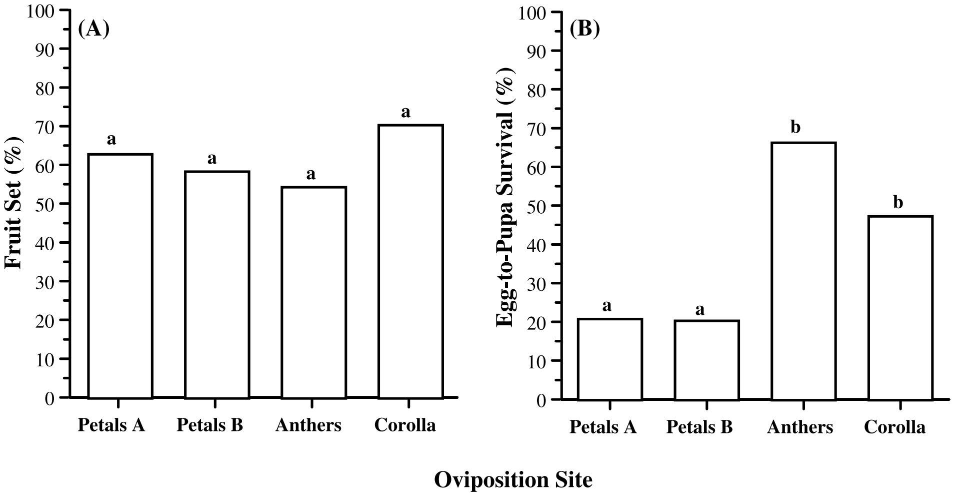

Fig. 3. Variation in fruit set, A (percent of flowers initiating fruit development given available resources), and egg-to-pupa survival, B, among four oviposition sites of adult senita moths on flowers of senita cacti: Petals A, Petals B, Anthers and Corolla tubes. For both fruit set and egg-to-pupa survival, oviposition sites with different letters are significantly different (chi-squared test for comparing multiple proportions; $\alpha = 0.05$; Zar, 1999).

1997; Fournet *et al.*, 2001). Below, we discuss potential ecological and evolutionary explanations why natural selection has apparently favoured oviposition behaviour that results in an even distribution of eggs among flowers, but has not more strongly favoured greater frequency of oviposition in anthers and corolla tubes where progeny survival is greatest.

Natural selection appears to have favoured the evolution of moth oviposition behaviour that results in a non-random, even distribution of eggs among flowers. This even egg distribution among flowers probably arises from individual moths not ovipositing multiple times within a single flower and moths avoiding laying eggs in flowers already oviposited by other individuals. Three factors, independently or collectively, may contribute to senita moths distributing their eggs evenly among flowers (i.e. one egg per flower). First, developing fruit are small, containing low-quantity, but high-quality, resources for larvae. An individual moth, or many moths, ovipositing multiple times into a single flower could lead to intraspecific competition between larvae for limited fruit food resources. Mortality effects of intraspecific competition may be particularly pronounced given that larvae do not move among fruit. Hence, selection may be strong for distributing eggs evenly among flowers to reduce intraspecific competition.

While variation in the quantity and quality of larval food resources both within and among host species can contribute to oviposition choice and larval performance, other factors may also influence oviposition behaviour and progeny survival. A second potential explanation for a non-random, even distribution of senita moth eggs among flowers relates to fruit abortion and risk-spreading behaviour by ovipositing moths. Senita cacti produce many more flowers than they have resources for developing mature fruit (Holland, 2002; Holland *et al.*, in press). Flowers in excess of resource-limited fruit set abort and fall off cacti before resource allocation to the fruit has begun. Consequently, eggs and larvae in aborted fruit die (Holland and Fleming, 1999). If fruit set is routinely resource-limited, as is the case for senita cacti (Holland and Fleming, 2002), then fruit abortion may be a significant source of mortality for pre-adult life stages. Moths that spread the risk of this mortality by laying eggs among many flowers, rather than in only a few flowers, may minimize the mortality effects of fruit abortion on their progeny. Similarly, senita moths may distribute their eggs evenly among flowers to reduce mortality resulting from density-dependent pupal mortality by an endoparasitic wasp (Holland and Fleming, 1999), as has been suggested for another seed-consuming moth species (Thompson, 1987).

Several sources of mortality could contribute to observed patterns in survivorship and differences among oviposition sites (Fig. 3), including in particular egg inviability, egg predation and the inhospitable environment of wilting corollas. Before discussing these sources of mortality in relation to oviposition sites, note that previous studies of cohort survivorship indicate that the large majority (> 80%) of pre-adult mortality occurs before the second larval instar (~6 days after eggs are laid) (Holland and Fleming, 1999; Holland, 2003). Of the more than 200 eggs that have been randomly collected from flowers, > 97% produced a first instar larva, indicating low egg inviability (Holland, 2003). Hence, the greater than 30% difference in survivorship between petals and anthers/corolla tube cannot be explained by egg inviability. Because eggs are laid on open flowers, they may be particularly vulnerable to predation, which itself could vary among oviposition sites. In particular, eggs laid on the upper, exposed surfaces of petals (petals B) may be more susceptible to predation than eggs underneath and between petals (petals A). Yet, egg-to-pupal survival was not different between eggs laid on these two areas of petals (Fig. 1B), suggesting that even if predation is common, it does not differ between oviposition sites petals A and B.

The most likely explanation for low egg-to-pupal survival for eggs laid on petals (both petals A and B; Fig. 3B) relates to the inhospitable environment of wilting corollas during the first few days when eggs hatch and larvae navigate down wilting corollas towards developing fruit (Holland, 2003). Two factors associated with wilting corollas contribute to lower egg-to-pupal survival for eggs laid on petals (both petals A and B) than for eggs laid on anthers and corolla tubes. First, eggs laid on anthers and within corolla tubes are much closer to the base of the corolla tube at the point of attachment to the developing fruit. This means less distance to navigate down the corolla tube and a shorter time required to do so. This shorter time period can be very important, as plant tissue at the corolla–fruit interface, through which larvae must bore to enter the fruit, hardens by 4–6 days after flower closing. Larvae requiring more time to navigate wilting corollas die at the base of the corolla because they are unable to bore through this hardened plant material (Holland and Fleming, 1999). Second, and probably more important, low survival of larvae of eggs laid on petals results from wilting petals becoming sticky and hard, making them difficult to navigate to bore into fruit. In contrast, first instar larvae hatching from eggs laid on anthers and corolla tubes can more easily navigate to fruit than larvae hatching from eggs in more direct contact with sticky, wilting petals. Although it has previously been suggested that egg predation was the primary cause of low egg survival (Holland and Fleming, 1999), this study and others (Holland, 2003; J.N. Holland, unpublished data) indicate that it is probably the inhospitable environment of the corolla, rather than egg predation, that reduces egg and first instar larva survival; this most likely accounts for differences in survival between oviposition sites of petals and anthers/corolla tubes.

Interpretation of the results for how selection has acted on oviposition choice among sites within flowers is not as clear-cut as with egg distribution among flowers. Two conflicting interpretations arise concerning selection for oviposition depending on whether or not surface area is incorporated into the analyses. Oviposition choice into anthers and corolla tubes and larval survival are positively correlated when surface area is accounted for, but negatively correlated when simply analysing frequency of eggs among sites. We suggest that selection is favouring oviposition into anthers and corolla tubes, given the disproportionately greater number of eggs in these sites when accounting for surface area. Yet, selection for oviposition into anthers/corolla tubes does not appear to be overwhelmingly strong, as the absolute raw number of eggs oviposited on petals far exceeds that of anthers and corolla tubes. It may simply be that petals are the first site encountered by moths, so that is where they most frequently lay their eggs.

Several reasons may contribute to why selection has not been stronger on oviposition into anthers and corolla tubes. First, the gene(s) determining oviposition behaviour in senita moths may exhibit some degree of negative pleiotropy with other phenotypic traits (Roff, 2002). It may be that increased survival resulting from selection for oviposition behaviour may at times reduce fitness to some degree by modifying another phenotypic trait due to negative pleiotropy. Second, adult performance and resource availability (Scheirs *et al.*, 2000; Reguera and Gomendio, 2002; Scheirs, 2002) may influence oviposition strategy and larval survival. Third, it may be that other sources of pre-adult mortality minimize the differential mortality effects of oviposition site. In particular, ~40% of eggs and larvae in this study died due to fruit abortion, regardless of oviposition site (Fig. 2A). However, it may be that the use of various floral parts for oviposition by senita moths is adaptive for reasons thus far not understood in cactus–moth interactions. If selection is acting on choice of oviposition sites in senita moths, the frequencies of eggs in anthers and corolla tubes are predicted to increase in future generations.

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