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## Geographic and population variation in pollinating seed-consuming interactions between senita cacti (*Lophocereus schottii*) and senita moths (*Upiga virescens*)

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**Abstract** Interspecific interactions can vary within and among populations and geographic locations. This variation can subsequently influence the evolution and coevolution of species interactions. We investigated population and geographic variation in traits important to pollinating seed-consuming interactions between the senita cactus (*Lophocereus schottii*) and its obligate pollinating moth (*Upiga virescens*), both of which are geographically restricted to the Sonoran Desert. Female moths actively pollinate senita flowers and oviposit onto flowers. Their larvae consume developing seeds and fruit of flowers pollinated by females. Traits important to this interaction include fruit set from moth pollination, fruit survivorship, and costs of fruit consumption by larvae. We studied these traits for five populations at two widely separated geographic locations. On average, 37% of flowers set fruit, 22% of flowers produced mature fruit, and larvae consumed 25% of immature fruit pollinated by female senita moths. Senita cactus and senita moth interactions were strongly mutualistic in all populations that we studied. Although one population had statistically lower fruit set and fruit production than the other four, all five populations were qualitatively similar in fruit production, costs, and patterns of fruit survivorship. Hand-pollination experiments suggested that fruit set was resource-limited in all but this one population. Apparent pollen limitation in the one population explains the quantitative differences in fruit set and fruit survivorship among the populations. As predicted by theory and exemplified by the senita mutualism, specialized and/or obligate interactions vary little among populations and geographic locations.

**Key words** Mutualism · Pollination · Fruit set · Senita · Interaction outcome

### Introduction

Recent studies of interspecific interactions have emphasized variation in traits and interaction outcomes within populations, among populations, and across geographic ranges because such variation contributes to the evolution and coevolution of these interactions (Thompson 1988, 1994a, 1994b, 1997; Cushman and Addicott 1991; Thompson and Pellmyr 1992; Bronstein 1994; Cushman et al. 1998). For mutualistic interactions, geographic and population variation in traits important to interactions are expected to vary less in specialized/obligate interactions than in less-specialized facultative interactions (Bronstein 1994). In more specialized/obligate interactions selection should be stronger on traits that maintain the interaction (Bronstein 1994). Nevertheless, ecological variability among communities and geographic locations may be expected to produce differences in selection pressures on traits in particular mutualisms at different locations (Thompson 1988, 1994a, 1994b, 1997; Thompson and Pellmyr 1992; Bronstein 1994).

Interactions between plants and pollinators whose larvae consume the fruit and/or seeds of flowers, including fig/fig wasps, yucca/yucca moths, senita/senita moths, *Trollius* and *Chiastocheta* flies, and *Lithophragma* plants and *Greya* moths, range from obligate to less-specialized diffuse interactions and from commensalism to mutualism. Interactions between figs and fig wasps are mutualistic, cosmopolitan in their geographic distribution, and are thought to be coevolved obligate interactions (Janzen 1979; Kjellberg et al. 1987; Bronstein 1988a, 1988b, 1992; Herre 1996). Similarly, yucca and yucca moth interactions, which occur throughout Mexico and the United States, are obligately mutualistic, and are also thought to be coevolved (Riley 1892; Addicott 1986; Pellmyr and Huth 1994; Pellmyr et al. 1996b). Whereas interactions between *Trollius europaeus* and *Chiastocheta* flies are obligately mutualistic, interactions between *Chiastocheta* flies and other species of *Trollius* at different geographic locations are facultative (Pellmyr 1989, 1992). The geographically widespread interactions

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between *Greya* moths and *Lithophragma* plants can vary from commensalism to mutualism depending on variation in the traits important to the interaction and local community structure (Thompson and Pellmyr 1992; Pellmyr and Thompson 1996; Pellmyr et al. 1996b; Thompson 1997). Interactions between senita cacti and senita moths were mutualistic for the one geographic location studied (Fleming and Holland 1998; Holland and Fleming 1999), but it is not known whether this interaction is mutualistic or even occurs in other populations and geographic locations.

Senita cactus and senita moth interactions are ecologically and evolutionarily similar to yucca/yucca moth and fig/fig wasp mutualisms: female moths are active pollinators whose larvae consume seeds/fruit of flowers they pollinated. The similarity among senita/senita moth, yucca/yucca moth, and fig/fig wasp interactions suggests that senita/senita moth interactions may be as specialized, obligate, and coevolved as are yucca and fig mutualisms. Thus, we predicted, as theory suggests (Bronstein 1994), that senita moths interact mutualistically with senita cacti throughout their geographic range and that traits important to this interaction are not highly variable. Traits important to these pollinating seed-consuming interactions include fruit set from pollination by female moths, fruit/seed consumption by larvae, and mature fruit production by plants. Fruit set and seed survival to maturity determine the magnitude of benefits to plants, while reduction in seed survivorship by larval consumption imposes a cost to plants. Furthermore, if fruit set is resource-limited, then some immature fruit are aborted; such fruit abortions may be a mechanism by which overexploitation of plants by the pollinator's larvae is limited and the ecological and evolutionary stability of these mutualisms can be maintained (Bronstein 1992; Pellmyr and Huth 1994; J.N. Holland and D.L. DeAngelis, unpublished work).

In this paper, we report on population and geographic variation in traits important to pollinating seed-consuming interactions between senita cacti and senita moths. For five populations at two geographic locations, we studied traits associated with the survivorship of flowers from anthesis to maturation, including fruit set, fruit production, and fruit consumption. We conducted hand-pollination experiments to determine whether fruit set was pollen- or resource-limited and estimated costs of fruit consumption. Although quantitative differences occurred among populations in fruit survivorship, the traits and outcomes of this mutualism were remarkably similar in all populations.

## Materials and methods

### Study species

Senita cacti, *Lophocereus schottii* (Engelm.) Britton and Rose, are restricted to the Sonoran Desert of Mexico and south-central Arizona, United States, and Baja California. Senita cacti attain heights of 2–4 m and have many branches radiating from their

base (Parker 1989). Areoles (small spine-bearing pads) near the tops of branches produce flowers from April through August. Flowers are hermaphroditic, self-incompatible, and remain open for <12 h. For the flowers setting fruit, 75–90% fruit set results from nocturnal pollination by senita moths; the remaining 10–25% fruit set results from diurnal pollination by halictid bees when flowers remain open after sunrise. During the first 6 days after flowers close, immature fruit abort and unpollinated flowers abscise due to pollen- and resource-limitation (Fleming and Holland 1998; Holland and Fleming 1999). Fruit mature c. 30 days after flowers close.

Senita moths, *Upiga virescens* (Hulst) (Lepidoptera: Pyralidae), are small moths (forewing 7–9 mm) restricted to the Sonoran Desert of Mexico and south-central Arizona, United States, and Baja California. All life stages of *U. virescens* are associated exclusively with senita cacti (Holland and Fleming 1999). Female moths actively pollinate senita flowers and oviposit an egg onto the flower. Larvae hatch from eggs, bore into developing fruit, and consume seeds and tissue of developing fruit when fruit are 6–16 days old. They then exit through the base of fruit at the point where the fruit is attached to the areole to pupate in the cactus branch. All seeds of fruit occupied by a larva are killed because exiting the fruit induces fruit abscission. Not all senita fruit are consumed by a larva because not all eggs hatch and produce surviving larvae.

### Study sites

During the flowering season in 1996, we studied cactus-moth interactions at two sites, Polilla Flats (PF) and Seri Flats (SF), near Bahia de Kino, Sonora, Mexico (Table 1). During the flowering season in 1997, we studied interactions at three sites, Senita Basin North (SBN), Senita Basin South (SBS), and Dos Republicas (DR), at Organ Pipe Cactus National Monument (OPCNM) in south-central Arizona (Table 1). Populations near Bahia de Kino are in the central portion of the range of senita cacti; cacti at OPCNM are the most northern populations of its distribution. The two geographic locations are separated by approximately 360 km. Populations within a geographic location were separated by 2–5 km. Senita cactus populations in the two geographic locations are quite distinct genetically; populations within a geographic location also exhibit substantial genetic differentiation but likely only represent sub-populations (Parker and Hamrick 1992; J. Hamrick, J. Nason, and T. Fleming, unpublished work).

### Fruit survivorship

We studied senita cactus flowers from anthesis to fruit maturation in order to assess fruit survivorship, fruit set, and fruit consumption by larvae. We labeled 1,154 flowers ( $n=30$  plants) at PF, 1,148 flowers ( $n=30$  plants) at SF, 1,086 flowers ( $n=22$  plants) at SBN, 1,090 flowers ( $n=20$  plants) at SBS, and 221 flowers ( $n=13$  plants) at DR. Sample size at DR was small because flower density and population size ( $n=17$  plants) were low at this site (Table 1). We censused closed flowers and immature fruit every 2–3 days to determine fruit survivorship. At PF, SBN, SBS, and DR fruit were censused every day for the first 6 days following flower closing to determine which flowers set fruit (at SF, fruit were only checked on days 3 and 6). We analyzed the proportion of fruit surviving among populations and geographic locations with a repeated-measures ANOVA using procedure GLM (SAS 1990). Differences in fruit set (day 6) and fruit production (day 30) were analyzed with an ANOVA and the Tukey's test was used to compare means of fruit set and fruit production among populations.

To investigate patterns of fruit set among populations and to determine whether fruit set was pollen- or resource-limited, we compared fruit set from hand-pollination experiments at SBN ( $n=22$  plants; 210 flowers), SBS ( $n=20$  plants; 211 flowers), DR ( $n=6$  plants; 45 flowers) and SF (Fleming and Holland 1998) with open-pollinated fruit set (day 6) from the fruit survivorship study.

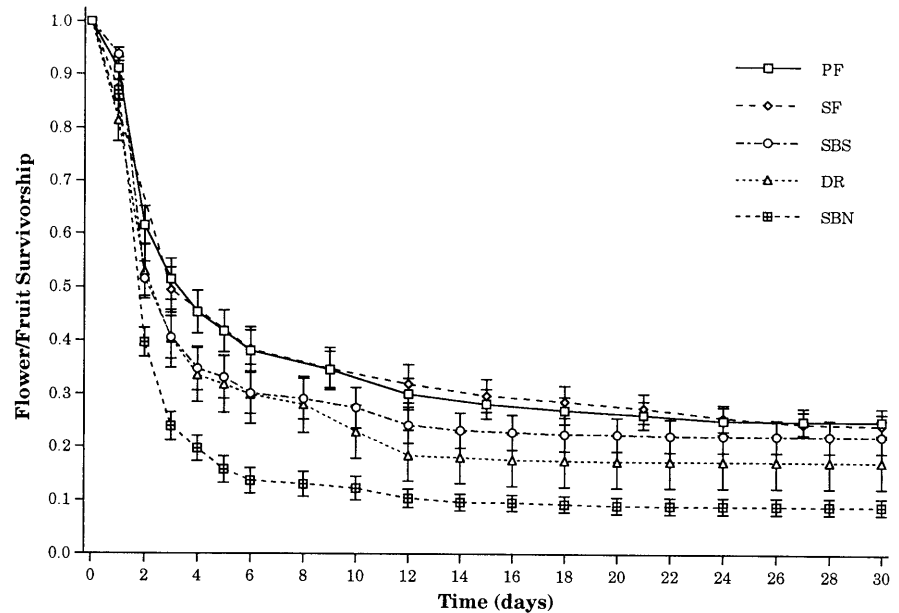
**Table 1** Geographic location and cactus density (number ha<sup>-1</sup>) for five senita populations where cactus-moth interactions were studied

Senita population	Acronym	Geographic location <sup>a</sup>	Latitude	Longitude	Cactus density
Polilla Flats	PF	Bahia de Kino	28°53'N	111°56'W	20.0
Seri Flats	SF	Bahia de Kino	28°52'N	111°57'W	7.7
Senita Basin North <sup>b</sup>	SBN	OPCNM	31°57'N	112°52'W	4.2
Senita Basin South <sup>b</sup>	SBS	OPCNM	31°56'N	112°53'W	1.1
Dos Republicas <sup>b</sup>	DR	OPCNM	31°54'N	112°51'W	0.4

<sup>a</sup> Bahia Kino, Sonora, Mexico, and Organ Pipe Cactus National Monument (OPCNM), Arizona, USA

<sup>b</sup> Cactus density for SBN, SBS, and DR are from Parker and Hamrick (1992)

**Fig. 1** Survivorship of flowers from anthesis (*day 0*) to fruit maturity (*day 30*) for senita cactus populations at PF (*n*=30 plants), SF (*n*=30 plants), SBS (*n*=20 plants), DR (*n*=13 plants), and SBN (*n*=22 plants). Symbols are mean proportions ( $\pm$  SE) of flowers/fruit surviving to a day. Abbreviations are as in Table 1



Stigmas of flowers on experimental plants were hand-pollinated using pollen of one fresh flower from another plant. Differences among populations in proportion fruit set (arcsine transformed due to small sample sizes) for hand-pollinated flowers were analyzed using procedure GLM (SAS 1990). Differences between open-pollinated and hand-pollinated fruit set within a population were analyzed using a *t*-test. Fruit set from hand-pollination treatments among SF, SBN, SBS, and DR were compared using a chi-square contingency test.

Costs to cacti for interacting with *U. virescens* were calculated from data on fruit survivorship. Cost per cactus was defined as the proportion of set fruit that did not reach maturity due to seed/fruit consumption by larvae. Larvae that survive to become seed/fruit consumers always induce fruit abscission when they exit fruit to pupate in cactus branches. Fruit abscission due to larval occupancy occurs when fruit are 6–16 days old (Fleming and Holland 1998; Holland and Fleming 1999). We used percent fruit destroyed instead of percent seeds destroyed as a response variable for costs since all seeds in fruit containing a larva are lost when a fruit abscises. Flowers closed before sunrise during these studies, thereby eliminating confounding effects of diurnal pollinators to cactus-moth interactions. We analyzed differences in costs among populations using a one-way ANOVA. We analyzed distributions of costs among cacti within each population using tests of skewness (D'Agostino and Tietjen 1973) and kurtosis (D'Agostino and Tietjen 1971; D'Agostino and Pearson 1973). Skewness and kurtosis statistics test for deviation from normality in the distribution of costs among individual cacti within a population. We performed skewness and kurtosis tests to compare variation among the populations in the distribution of costs.

## Results

Fruit survivorship on senita cacti reflects three traits important to cactus-moth interactions: fruit set from pollination by female moths, fruit consumption by larvae of moths during days 6–16, and the maturation of fruit by day 30. For all study populations, fruit survival decreased through day 14, but then remained relatively constant until day 30 when fruit ripened (Fig. 1). Although all study populations had similar overall patterns in fruit survivorship, significant quantitative differences did occur in fruit survivorship among the populations (Fig. 1; repeated measures ANOVA, time $\times$ population,  $F_{20,550}=3.26$ ,  $P=0.0029$ ). Also, significant differences occurred among populations in the production of mature fruit (one-way ANOVA,  $F_{4,110}=6.18$ ,  $P=0.0002$ ). Proportion of flowers producing mature fruit at SBN differed significantly from PF, SF, and SBS, but no other differences in mature fruit production occurred among the populations (Tukey's test,  $P<0.05$ ). About 10% of flowers produced mature fruit at SBN, whereas on average 22% of flowers produced mature fruit in the other populations (Fig. 1).

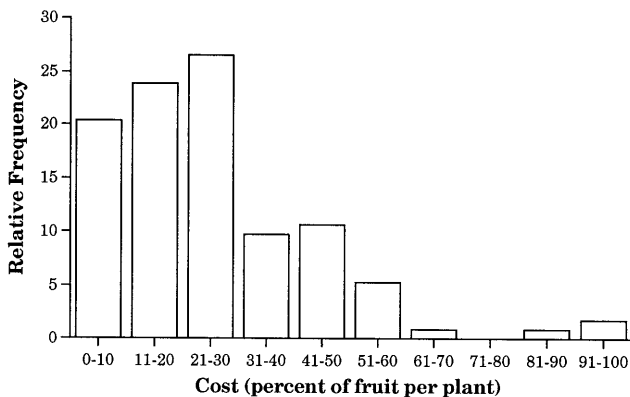
Similarly, significant differences occurred among populations in fruit set (i.e., the fraction of flowers sur-

**Table 2** Costs to cactus populations for interacting with senita moths. Mean±SE, median, and range of proportion of set fruit abscising due to fruit/seed consumption by larvae of *Upiga virescens* for senita cactus populations at PF ( $n=30$  plants), SF ( $n=30$  plants), SBS ( $n=20$  plants), DR ( $n=12$  plants), and SBN ( $n=21$

Population	Mean±SE	Median	Range	Skewness	Kurtosis
PF	0.27±0.029 ab	0.24	0–0.60	0.240 <sup>a</sup>	–0.457 <sup>b</sup>
SF	0.19±0.026 b	0.19	0–0.53	0.588 <sup>a</sup>	1.120 <sup>b</sup>
SBN	0.23±0.047 ab	0.25	0–0.67	0.356 <sup>a</sup>	–1.034 <sup>b</sup>
SBS	0.25±0.035 ab	0.23	0–0.57	0.451 <sup>a</sup>	–0.308 <sup>b</sup>
DR	0.43±0.105 a	0.29	0–1.00	0.584 <sup>a</sup>	–1.055 <sup>b</sup>

<sup>a</sup> No significant deviation from normality ( $P>0.05$ , D'Agostino and Tietjen 1973)

<sup>b</sup> No significant deviation from normality ( $P>0.05$ , D'Agostino and Tietjen 1971, D'Agostino and Pearson 1973)



**Fig. 2** Relative frequency (percentage) of costs for all individuals ( $n=113$  plants) among the five study populations. Costs are the proportion of fruit per plant abscising due to consumption by senita larvae. Costs for individual plants are grouped in intervals of 10%

living as immature fruit to day 6; Fig. 1; one-way ANOVA,  $F_{4,110}=6.62$ ,  $P=0.0001$ ). As with fruit production, PF, SF, SBS, and DR did not differ significantly in fruit set, but SBN set significantly fewer fruit than PF, SF, and SBS (Tukey's test,  $P<0.05$ ). Among the populations studied (SF, SBN, SBS, and DR), there were no differences in fruit set of hand-pollinated flowers ( $\chi^2=3.31$ ,  $df=3$ ,  $P=0.346$ ). Proportion of flowers setting fruit after hand pollination at SF, DR, SBN, and SBS was 0.464, 0.396, 0.353, and 0.435, respectively. In comparing open-pollinated and hand-pollinated fruit set within a population, a significant difference occurred only at SBN ( $t=3.64$ ,  $df=32$ ,  $P<0.05$ ), suggesting pollen-limited fruit set for this population (but see Zimmerman and Pyke 1988). Pollen limitation in the SBN population accounts for its lower fruit set, its lower fruit production, and the quantitative differences among the populations in overall fruit survivorship (Fig. 1).

Cost to senita cacti from interacting with senita moths was defined as the proportion of flowers setting fruit that were subsequently destroyed by larvae. Fruit abscissions induced by larvae occur during days 6–16 after flowers close. After day 12, fruit consumption and larval-induced fruit abscission begin to cease, causing fruit sur-

plants) (populations are abbreviated as in Table 1). Skewness and kurtosis of costs for each population are presented as measures of the distribution of costs among cacti within a population. Means followed by different non-superscript letters are significantly different (Tukey's test,  $P<0.05$ )

ivorship to level off as larvae enter cactus branches (Fig. 1; Fleming and Holland 1998; Holland and Fleming 1999). The proportion of set fruit consumed by larvae ranged from <20% at SF to >40% at DR (Table 2). These two populations differed significantly in the proportion of fruit consumed, but no other differences in costs occurred among populations (Table 2;  $F_{4,108}=3.23$ ,  $P=0.0152$ ; Tukey's test). The distribution of costs among individual cacti within each population were not significantly skewed or kurtotic; for all five study populations, costs were normally distributed among cacti (Table 2). On average,  $25\pm 1.8\%$  ( $\pm$ SE) of fruit set was consumed by larvae. Of the 113 individual cacti in which costs were measured, the modal cost was 0% (not to be confused with the modal range of 21–30%): 15% of all individual cacti incurred no cost. Costs were <10% in 20% of the individuals and were <30% in 70% of all individuals (Fig. 2). Senita cactus and senita moth interactions were mutualistic, even at DR where costs were greater than in other populations. Thus, while one quantitative difference in cost occurred among the populations, senita cactus and senita moth interactions were qualitatively similar (i.e., mutualistic) among populations and geographic locations.

## Discussion

The outcome of interactions between plants and their pollinating seed-consumers depends, in part, on three traits associated with fruit survivorship: fruit set, fruit consumption by larvae of the pollinators, and fruit/seed production. Our study of fruit survivorship for senita cacti showed low variation in these traits, and senita/senita moth interactions were qualitatively similar among populations at the center of the species' geographic range (Bahia de Kino) and at the edge of their geographic range (OPCNM). This study thus demonstrates that mutualistic interactions between senita cacti and senita moths are not restricted to the one geographic location previously studied (Fleming and Holland 1998; Holland and Fleming 1999). Quantitative differences in fruit survivorship and fruit production are explained by pollen-limited fruit set in the SBN population.



The lack of substantial variation in fruit survivorship, fruit set, and fruit consumption among the populations that we studied supports theoretical predictions for specialized and/or obligate interactions. For obligate mutualisms, as compared to facultative mutualisms, selection pressures should be stronger on traits important to the maintenance of positive interactions (Bronstein 1994). Furthermore, if selection pressures are similar among populations, then variability of that trait within a population may be expected to be similar among populations. One trait important to the outcome and maintenance of interactions between plants and pollinating seed-consumers is the cost to plants of fruit consumption by larvae. As stated by Thompson (1988, p. 65), "just as variation in traits in populations is the raw material for the evolution of species, variation in outcome is the raw material for the evolution of interactions." Among the populations where senita/senita moth interactions were studied, the outcome of interactions were mutualistic and costs were similarly low and invariable. As indicated by the absence of skewness and kurtosis, the distribution of costs among individual plants within a population was similar among populations (Table 2). The lack of substantial variation among populations in costs and the distribution of costs within a population suggest similar selection pressures on factors influencing costs of senita cactus and senita moth interactions. This lack of variation is consistent with what is predicted for specialized/obligate interactions.

Costs to plants among populations are similar for senita/senita moth and yucca/yucca moth interactions. For both senita and yucca, most fruit and plants have low costs (<30%) (Addicott 1986; Pellmyr et al. 1996a; Holland and Fleming 1999; Table 2). Furthermore, many fruit (30–80%) of senita and yucca have no cost, that is, no seeds were consumed by larvae (Keeley et al. 1984, 1986; Addicott 1986; Holland and Fleming 1999; Fig. 2). The lack of costs for a fruit may be explained by egg/larval mortality and/or failed ovipositions (Keeley et al. 1984, 1986; Addicott 1986; Pellmyr and Huth 1994; Holland and Fleming 1999). Further research is needed to determine if low survival of senita moth and yucca moth eggs and larvae is due to infertility, predation, or some other factor. Nevertheless, it is becoming increasingly apparent that life-history traits (e.g., mortality) can be important factors contributing to the low costs to senita and yucca for interacting with their obligate pollinators.

Not only are there similarities in costs among senita populations and among yucca populations and species, but senita and yucca plants also lack substantial variation in fruit set. Resource-limited fruit set is common in senita cacti and species of yucca (Udovic 1981; Udovic and Aker 1981; Fuller 1990; Pellmyr and Huth 1994; Richter and Weis 1995; Huth and Pellmyr 1997; Fleming and Holland 1998; Holland and Fleming 1999; Fig. 1). Resource-limited fruit set can allow plants to selectively abort immature fruit containing low quality or low quantity of seeds (Stephenson 1981; Lee 1984; Stephenson and Winsor 1986; Becerra and Lloyd 1992; Pellmyr and

Huth 1994; Huth and Pellmyr 1997). Aborting fruit is a mechanism by which plants can match fruit production to available resources under a variety of resource levels (Stephenson 1981). However, for resource-limited senita cactus populations, no significant differences occurred in fruit set among populations. On average, only 37% (range 30–46%) of flowers set fruit. Similarly, on average 8% (range 3–14%) of flowers set fruit in different *Yucca* populations and species throughout their geographic range (Schaffer and Schaffer 1979; Udovic 1981; Udovic and Aker 1981; Aker 1982a, 1982b; Kingsolver 1984; Fuller 1990; James et al. 1993, 1994; Pellmyr and Huth 1994; Huth and Pellmyr 1997; Addicott 1998).

Why is variation in fruit set so low in senita and yucca plants? It is unlikely that the abundance of resources responsible for limiting fruit set is similar among populations and species across the wide geographic distribution of *Yucca* or throughout the Sonoran Desert where senita occur. Alternatively, because survival of pollinating seed-consumers is directly influenced by fruit abortions (Richter and Weis 1995; Wilson and Addicott 1998; Holland and Fleming 1999), plants may be able to regulate pollinator populations and fruit production through low levels of fruit set (Udovic 1981; J.N. Holland and D.L. DeAngelis, unpublished work). By decreasing pollinator numbers through reduced fruit set, fewer eggs are oviposited, the number of fruit/seeds consumed by pollinator larvae decreases, and fruit production may actually increase compared with no fruit abortion (J.N. Holland and D.L. DeAngelis, unpublished work).

In conclusion, we wish to emphasize that our estimates of costs and fruit set are only point-estimates for a long-lived cactus that interacts with many cohorts of moths. Fruit set and costs to individual cacti and cactus populations as a whole may fluctuate through time with moth population dynamics. Nonetheless, this study, along with our previous studies (Fleming and Holland 1998; Holland and Fleming 1999), demonstrates that senita cactus and senita moth interactions have similar traits and outcomes across populations and years, and over a wide geographic area.

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