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Benefits and costs of mutualism: demographic consequences in a pollinating seed–consumer interaction

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Interspecific interactions can affect population dynamics and the evolution of species traits by altering demographic rates such as reproduction and survival. The influence of mutualism on population processes is thought to depend on both the benefits and costs of the interaction. However, few studies have explicitly quantified both benefits and costs in terms of demographic rates; furthermore there has been little consideration as to how benefits and costs depend on the demographic effects of factors extrinsic to the interaction. I studied how benefits (pollination) and costs (larval fruit consumption) of pollinating seed-consumers (senita moths) affect the reproduction of senita cacti and how these effects may rely on extrinsic water limitation for reproduction. Fruit initiation was not limited by moth pollination, but survival of initiated fruit increased when moth eggs were removed from flowers. Watered cacti produced more flowers and initiated more fruit from hand-pollinated flowers than did unwatered cacti, but fruit initiation remained low despite excess pollen. Even though water, pollination and larvae each affected a component of cactus reproduction, when all of these factors were included in a factorial experiment, pollination and water determined rates of reproduction. Counter-intuitively, larval fruit consumption had a negligible effect on cactus reproduction. By quantifying both benefits and costs of mutualism in terms of demographic rates, this study demonstrates that benefits and costs can be differentially influential to population processes and that interpretation of their influences can depend on demographic effects of factors extrinsic to the interaction.

Keywords: demography; extrinsic factors; flower/fruit ratio; water resource limitation; senita cacti

1. INTRODUCTION

Interspecific interactions can affect population processes, such as population dynamics and the evolution of species traits (Park 1948; Huffaker 1958; Pimentel & Al-Hafidh 1963; Pimentel *et al.* 1965; Varley *et al.* 1973; Thompson 1982; Hanzawa *et al.* 1988), by altering per capita rates of reproduction and survival. Such changes in demographic rates can in turn affect population growth rates and the mean fitness of individuals (Fisher 1930; Lande 1982). Influences of mutualism on population processes are thought to depend on both benefits and costs of the interaction (Boucher 1985). Benefits include nutrient acquisition, transport of oneself or one's gametes and protection from biotic and abiotic elements. Costs are investments in structures and substances that attract and reward mutualists. Even though benefits and costs are central to the study of mutualism (Addicott 1986; Pierce *et al.* 1987; Pellmyr & Huth 1994; Herre *et al.* 1999; Bronstein 2001), little can be said about their general effects on population processes. This is in part because the types of benefits and costs vary so greatly within and among mutualisms that there is little consensus on the currency in which to quantify them.

Quantifying benefits and costs in demographic currencies can directly link benefits and costs with mutualism's effects on population processes, because many population processes are largely determined by rates of reproduction and survival. Nevertheless, demographic rates of species involved in mutualisms are rarely determined solely by the benefits and costs of that mutualism. Influences of benefits and costs may depend on the demographic effects of factors extrinsic to interactions. When evaluating how mutualisms and interspecific interactions in general affect populations, it is important to consider biotic and abiotic factors extrinsic to interactions (Varley *et al.* 1973; Holt 1977; Horvitz & Schemske 1984; Thompson & Pellmyr 1992; Abrams *et al.* 1998). Otherwise, results may yield misleading conclusions about the effects of benefits and costs of mutualism on populations.

To my knowledge, no study of mutualism has explicitly evaluated the effects of both benefits and costs on demographic rates, or considered how these effects may depend on demographic effects of factors extrinsic to that interaction. I attempted such a study using the pollinating seed–consumer mutualism between senita cacti and senita moths. Fruit initiation by senita cacti is increased by the benefits of moth pollination, while immature fruit survival is reduced by the costs of larval fruit consumption. Yet, these effects may rely on extrinsic limitation of water resources for cactus reproduction. Through separate experiments, I studied the effects of moth pollination on fruit initiation, larval fruit consumption on immature fruit survival and water limitation on flower production and fruit initiation. Then, in a factorial experiment, I studied the independent and combined effects of water, pollination and larval fruit consumption on cactus reproduction.

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2. METHODS AND STUDY SYSTEM

(a) *System of study: the senita mutualism*

I studied interactions between senita cacti (*Lophocereus schottii*; Cactaceae) and senita moths (*Upiga virescens*; Pyralidae) from 1998–2000 near Bahia de Kino, Sonora, Mexico. Senita cacti are long-lived plants (more than 50 years) that produce self-incompatible, hermaphroditic flowers from April to September. Female senita moths lay their eggs in flowers and are the exclusive nocturnal pollinator. Other flower visitors (bees) are rarely important to cactus reproduction (Holland & Fleming 1999*a*,*b*, 2002). Larvae of senita moths consume some immature fruit. Not all fruit are destroyed by larvae, however, because not all flowers receive eggs and not all eggs and larvae survive to consume fruit. Also, resource limitation prevents some pollinated flowers from initiating fruit (Fleming & Holland 1998; Holland & Fleming 1999*a*,*b*). Thus, reproduction by cacti appears to be determined primarily by moth pollination, larvae and resource limitation.

(b) *Water-addition treatments*

I watered senita cacti to assess whether water limited flower production, fruit initiation, immature fruit survival and mature fruit production. I indiscriminately chose 50 plants throughout my 20 ha study site, 25 plants for controls and 25 plants for watering. Soil walls of 0.3 m in height and 5.3 m (± 0.2 s.e.) in diameter were built around 25 cacti to prevent run-off. Roots of senita cacti grow deep into the soil to utilize water percolating through the soil column (Cody 1986). I added *ca.* 4600 l of water to each of 25 cacti preceding the 1999 and 2000 flowering season. To mimic natural patterns in annual rainfall, I added *ca.* 65% of this volume in summer (July) and *ca.* 35% in winter (December). Water addition was equivalent to 213 ± 14 mm (± 1 s.e.) of rain for the 1999 flowering season and 229 ± 15 mm (± 1 s.e.) of rain for the 2000 flowering season. Mean annual rainfall at Bahia de Kino between 1974 and 1993 was 126.4 ± 72 mm (± 1 s.d) and ranged from 43–279 mm (DICTUS, Bahia de Kino, Sonora, Mexico). Watering did not exceed 2 s.d. of mean annual rainfall. In 1999, watered plants had a greater percentage of water content than unwatered plants, as measured by tissue of cactus ribs (95% confidence interval (CI) of difference, 6.5 ± 0.02; one-tailed t-test, $t = 7.05$, d.f. = 48, $p < 0.0001$), but in 2000 these differences were not as great (one-tailed t-test, $t = 1.36$, d.f. = 42, $p < 0.09$). The observed difference in 2000 was 0.9% and the minimal detectable difference was 1.9%, for a statistical power of 0.8 at $\alpha = 0.05$ (Zar 1999).

(c) *Flower production*

For 25 watered and 25 control cacti, I counted newly opened flowers per plant every day for the 1999 flowering season and once a week for the 2000 flowering season. Total flower production per plant was estimated by integrating the area under the flower phenology curve. Differences in flower production between watered and control plants were analysed with a pooled-variance t-test.

(d) *Resource- versus pollen-limitation experiments*

I examined the resource-limited fruit set for watered and unwatered plants in June and July 1999 and June 2000 by quantifying fruit set of flowers supplemented with excess outcrossed pollen. This assured no pollen limitation and isolated the effects of water. An excess of pollen was added to stigmas by brushing them with anthers from newly dehisced flowers of another plant. In 1999 and 2000, I counted seeds in each of three to five fruit from each of the watered and unwatered plants. Mean seed production per fruit per plant was then analysed for the effects of time and treatment. Fruit set and seed production were analysed using repeated-measures ANOVAs.

(e) *Seed and fruit consumption by moth larvae*

To assess the effects of larvae on survival of immature fruit, I manipulated larval fruit consumption by removing all eggs from individual flowers. I compared the survival of those flowers setting fruit for 19 plants (*ca.* 30 fruit per plant) with 24 control plants (*ca.* 30 fruit per plant) from which no eggs were removed from flowers, using a one-way ANOVA and Tukey's test.

(f) *Factorial experiment*

In a fully crossed factorial experiment, I assessed how pollination, larval fruit consumption and water resources contribute separately and multiplicatively to fruit set, immature fruit survival, fruit maturation and flower-to-fruit longevity. Fruit set and immature fruit survival represent the two stages between flowers and mature fruit, while fruit maturation and flower-to-fruit longevity are cumulative measures of cactus reproduction. For the pollination treatment, I supplemented flowers with excess pollen as described above (see § 2d). For the larval treatment, I removed eggs from flowers. For the resource treatment, I added water to cacti as described above (see § 2b). For each factor, two levels were established: treatments (excess pollen, egg removal, water addition) and controls (open-pollinated flowers, no egg removal, no water added). Treatments were randomly assigned to plants; sample sizes ranged from five to seven plants. I included *ca.* 60 flowers per plant for a total of 3046 flowers. I quantified four response variables: (i) fruit set, proportion of flowers initiating fruit 6 days after anthesis; (ii) immature fruit survival, proportion of set fruit surviving to fruit maturation; (iii) fruit maturation, proportion of flowers surviving 20 days after anthesis; and (iv) flower-to-fruit longevity, the age to which flowers or fruit survived. Each response variable was analysed with a multifactor ANOVA (Proc Glm; SAS Institute 1999). Proportions were not arcsine transformed because, due to large samples of flowers, response variables were normally distributed. Because no first- or second-order interaction was significant, interaction terms were removed to increase the degrees of freedom (d.f.). This did not change the interpretation of any analysis, only the size of F- and p-values for the overall model.

3. RESULTS

(a) *Flower production*

In both 1999 and 2000 (figure 1), watered plants produced significantly more flowers than did unwatered plants (1999, $t = 4.525$, d.f. = 48, $p < 0.0001$; 2000, $t = 4.352$, d.f. = 48, $p < 0.0001$). On average (± 1 s.e.), watered plants produced two-and-a-half to three times more flowers than unwatered plants (3415 ± 456 and 1238 ± 152 flowers, respectively, in 1999, and 2966 ± 354 and 1247 ± 174 flowers, respectively, in 2000). The 95% CI for the mean difference between watered and unwatered plants was 2177 ± 961 flowers in 1999 and 1719 ± 790 flowers in 2000.

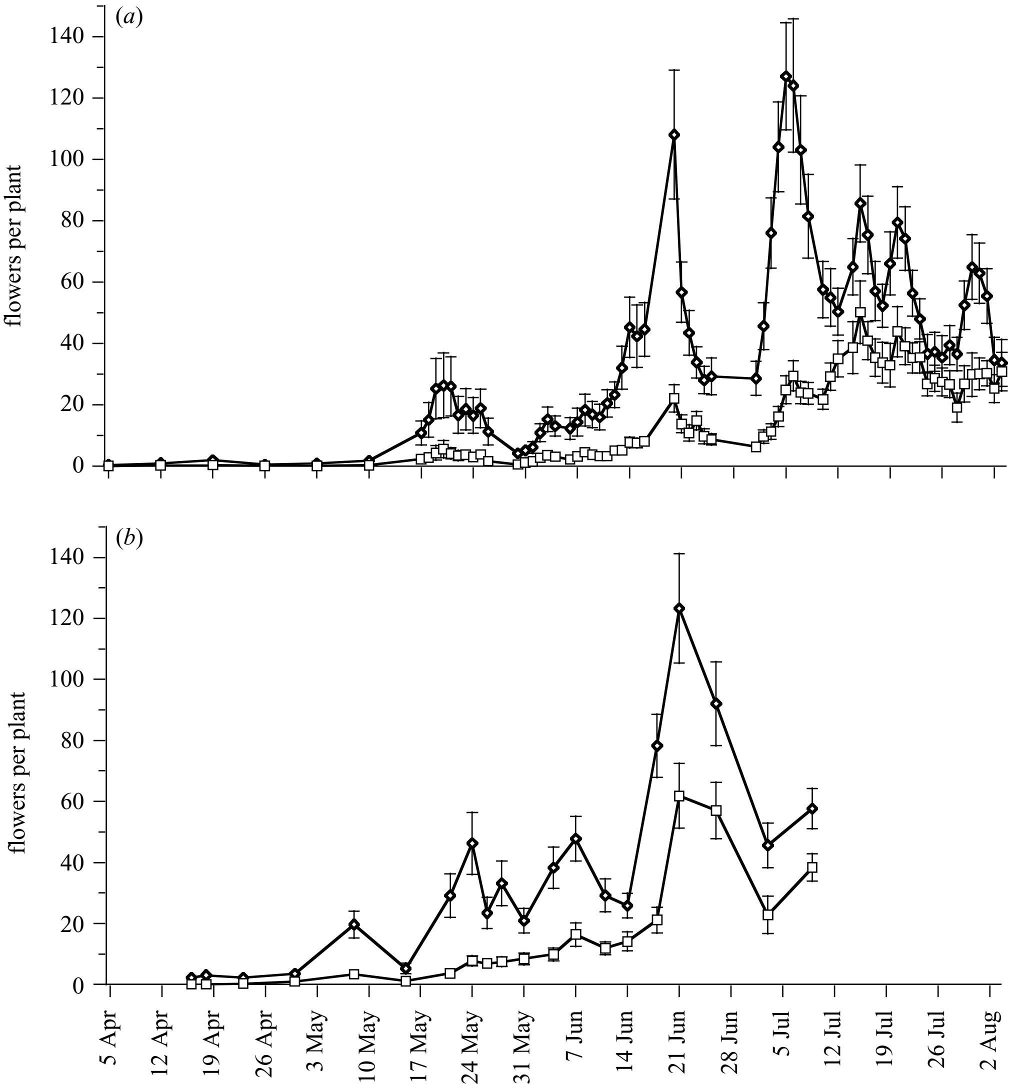

Figure 1. Phenology of flower production (number of flowers per plant (mean ± 1 s.e.); $n = 25$ plants) for water-addition plants (diamonds) and control plants (squares) in (*a*) 1999 and (*b*) 2000.

(**b**) *Resource- versus pollen-limited fruit set and seed production*

There was no significant interaction between the watering treatment and time on fruit set (June and July 1999) (figure 2*a*; repeated-measures ANOVA, $F_{1,46} = 0.30$, $p > 0.58$) and no significant main effect of time on fruit set (figure 2*a*; repeated-measures ANOVA, $F_{1,46} = 1.71$, $p > 0.19$). In 1999 and 2000, watered and unwatered plants initiated fruit in only a subset of their flowers, despite sufficient pollen, indicating that fruit set was limited by resources rather than pollen (figure 2*a*). In June and July 1999, watered plants initiated more fruit than unwatered plants (figure 2*a*; repeated-measures ANOVA, $F_{1,46} = 3.97$, $p = 0.052$, $\alpha = 0.10$). In June 2000, I again found a significant positive effect of water on fruit set (figure 2*a*; $t = 2.88$, d.f. = 28, $p < 0.01$, $\alpha = 0.10$). Fruit set was greater in 2000 than in 1999, probably due to the first substantial rain event in 5 years on 6 March 2000.

No significant interaction occurred between watering treatment and time (1999 and 2000) for seed production (figure 2*b*; repeated-measures ANOVA, $F_{1,48} = 0.01$, $p > 0.90$). Seed production for watered plants was significantly greater than for control plants (figure 2*b*; repeated-measures ANOVA, $F_{1,48} = 6.98$, $p < 0.02$). Seed production in 2000 was significantly greater than in 1999, proabably due to rain on 6 March 2000 (figure 2*b*; repeated-measures ANOVA, $F_{1,48} = 4.18$, $p = 0.046$).

(**c**) *Seed consumption by moth larvae*

Survival of initiated fruit through fruit maturation was increased (69% versus 85%) by removing eggs from flowers (ANOVA, $F_{1,41} = 4.92$, $p = 0.032$).

(**d**) *Factorial experiment*

Water resources significantly increased fruit set, but pollen supplementation did not increase fruit set (table 1; figure 3). After correcting for experimentwise error rate, egg removal did not affect fruit set. Egg removal did, however, significantly increase immature fruit survival by reducing larval fruit consumption. As expected (Stephenson 1981), neither water addition nor pollen supplementation significantly affected the survival of set fruit to fruit maturation.

Effects of water, pollination and larval fruit consumption were consistent for the two separate cumulative measures of overall rates of cactus reproduction (i.e. fruit

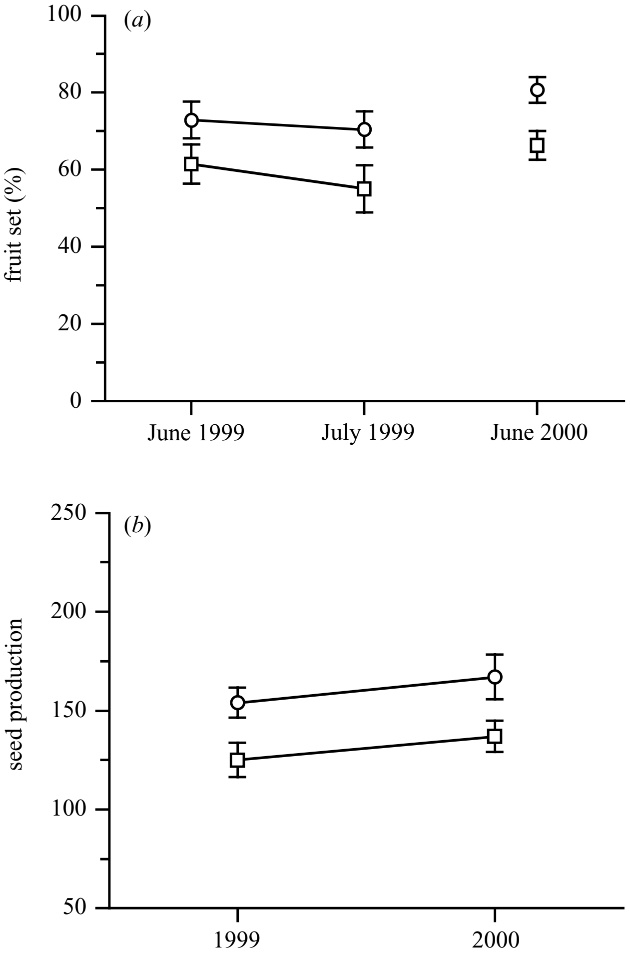

Figure 2. (*a*) Percentage fruit set (mean ± 1 s.e.; $n = 20$–25 plants) of hand-pollinated flowers for water-addition plants (circles) and control plants (squares) in June and July 1999 and June 2000. (*b*) Seed production per fruit per plant (mean ± 1 s.e.; $n = 25$ plants) for water-addition plants (circles) and control plants (squares) in 1999 and 2000.

maturation and flower-to-fruit longevity; table 1; figure 3). There was a 19% difference in fruit maturation between watered and unwatered plants, a 10% difference between plants with pollen-supplemented flowers and plants with open-pollinated flowers, and a 1% difference between egg-removal plants and plants with eggs intact. Only water increased the overall rate of cactus reproduction. Pollen supplementation did not significantly increase reproduction, even for watered plants. Although larval consumption of fruit significantly reduced the survival of immature fruit, this had no significant effect on the overall rate of cactus reproduction. The minimum detectable difference for the effects of egg removal on fruit maturation in this multifactor experiment was 11% (statistical power, 0.8; $\alpha = 0.05$; Zar 1999).

4. DISCUSSION

Benefits and costs represent a fundamental foundation on which mutualisms are investigated and interpreted (Roughgarden 1975; Addicott 1986; Cushman & Beattie 1991; Herre *et al.* 1999; Bronstein 2001). However, there is little understanding of benefits and costs beyond the general notion of their qualitative effects. Generalizations have been hindered by the high diversity in the kinds of benefits and costs that exist both within and among mutualisms, as well as inconsistencies in currencies used to measure them. Nevertheless, mutualism affects population processes (e.g. population growth and evolution of species traits) through the effects of benefits and costs on reproduction and survival. However, these effects may rely on demographic effects of factors extrinsic to an interaction. In this study, I manipulated benefits and costs and measured them in the demographic currency of reproduction while simultaneously considering the demographic effect of extrinsic water limitation. To my knowledge, this study provides some of the first experimental evidence that the benefits and costs of mutualism can be differentially important to population processes and that their influences can rest on the demographic effects of factors extrinsic to the interaction.

In separate experiments, I examined the effects of: (i) benefits of senita moth pollination; (ii) costs of larval fruit consumption; and (iii) extrinsic water limitation on fruit set and immature fruit survival of senita cacti. Pollen supplementation did not increase fruit set. Senita moths have been abundant and effective enough to pollinate as many flowers as could set fruit, even when water increased the fruit set (this study; Holland & Fleming 1999*a*,*b*, 2002). The costs of larval feeding reduce survival of immature fruit by 15–29% (this study; Holland & Fleming 1999*a*,*b*). Finally, water limits flower production, fruit set and seed production. Greater seed production per fruit for watered than for unwatered cacti indicates that water limits either ovule production per flower or development of ovules into seeds. In a fully crossed factorial experiment, I then re-examined the separate effects of water, pollination and larval fruit consumption on individual components of cactus reproduction. The individual effects of these three factors were consistent among the factorial experiment and the separate, independent experiments.

The separate effects of water, pollination and larval feeding on individual components of cactus reproduction are suggestive of their effects on overall rates of reproduction. However, overall reproduction is determined by the multiplicative effects of water, moth pollination and larval feeding on fruit set and survival of immature fruit. When all three factors were measured in terms of overall reproduction in the fully crossed factorial experiment, cactus reproduction was determined only by water limitation and benefits of senita moth pollination. Costs of larval fruit consumption were negligible in explaining variation in reproduction among cacti, indicating that larval feeding did not limit reproduction. The large effect of water and pollination, and the minimal effect of larvae, are exacerbated by the fact that watered cacti produced more flowers than did unwatered cacti.

Before discussing these results, I consider two caveats to interpreting this study. First, the minimum detectable difference for the effects of egg removal on fruit maturation was 11%. It is feasible that larvae reduced cactus reproduction, but that it was less than an 11% reduction. In either case, larval feeding affected reproduction much less than water and pollination. The other caveat is the marginal p-value for the effect of egg removal on fruit set (table 1). After correcting for experimentwise error rate, this p-value is not significant. If experimentwise error rate

Table 1. Results of multifactor ANOVA for the effects of water addition, pollen supplementation and egg removal on fruit set (initiated fruit/flower), immature fruit survival (mature fruit/initiated fruit), fruit production (matured fruit/flower) and flower-to-fruit longevity (average age to which a flower survived from anthesis to fruit maturation).
(Pollen supplementation is equivalent to increasing the benefits of senita moth pollination, and egg removal is equivalent to reducing costs of larvae. None of the first- and second-order interactions was significant for any of the four analyses; *p*-values were more than 0.17 and most were near 0.50. The experimentwise error rate was corrected by the Dunn–Sidak method (Sokal & Rohlf 1995); *p*-values are significant if less than 0.034, denoted by an asterisk.)

response variable	source	d.f.	MS	*F*	*p*
fruit set	water addition	1	0.7272	13.75	0.0006*
	pollen supplement	1	0.0204	0.39	0.5377
	egg removal	1	0.2264	4.28	0.0442
	error	46	0.0529		
immature fruit survival	water addition	1	0.0023	0.10	0.7516
	pollen supplement	1	0.0531	2.39	0.1303
	egg removal	1	0.1168	5.25	0.0275*
	error	39	0.0223		
mature fruit	water addition	1	0.4193	9.47	0.0035*
	pollen supplement	1	0.1253	2.83	0.0993
	egg removal	1	0.0073	0.16	0.6875
	error	46	0.0442		
flower-to-fruit longevity	water addition	1	234.50	11.41	0.0015*
	pollen supplement	1	26.09	1.27	0.2657
	egg removal	1	16.96	0.83	0.3684
	error	46	20.55		

was ignored and the *p*-value interpreted as significant, then the only explanation for egg removal decreasing fruit set is that flowers were sensitive to handling. However, similar handling of flowers during hand pollinations did not decrease fruit set. There is neither a statistically nor biologically meaningful reason to interpret egg removal as reducing fruit set.

In this study, water resources and pollination determined reproduction in senita cacti. This result is not surprising. It is well known that both pollination and resources, particularly water in desert plants, can limit plant reproduction (e.g. Cunningham *et al.* 1979; Delph 1986; Herrera 1991; Mitchell 1994, 2001; Murren & Ellison 1996; Mothershead & Marquis 2000). While this study confirms prior work, it also yields some novel implications about benefits and costs of mutualism. Recall that, given extrinsic water limitation, benefits of moth pollination affected reproduction more than costs of larval feeding. One implication is that the demographic effect of factors extrinsic to an interaction can influence the relative effects of benefits and costs on demographic rates, and hence the mutualistic outcome of an interaction. In this study, water limitation masked the costs of mutualism. However, extrinsic factors may mask the benefits of mutualism, such that costs equal or outweigh benefits, causing a shift to parasitism or commensalism (Thompson & Pellmyr 1992). Just as the interaction strength of competition and predation can vary within and among interspecific interactions (Paine 1980, 1992; de Ruiter *et al.* 1995), so can the interaction strength of mutualism, due to variation in the demographic effects of benefits and costs. Finally, I suggest that, because larval fruit consumption had a negligible effect on plant reproduction, interpreting the influence of benefits and costs on population processes may depend upon quantifying their effects on demographic rates and in light of demographic effects of extrinsic factors. It may be best not to rigidly categorize and interpret benefits and costs, as such, as I previously did for larval fruit consumption, when benefits and costs may be conditional in space and time.

At first, it may appear counter-intuitive for larval fruit consumption to reduce immature fruit survival but not reduce overall reproduction. However, when assessing how multiplicative factors affect response variables, one or two of several factors may explain most of the variance. The factorial experiment in this study is analogous to the key-factor analysis carried out by Varley *et al.* (1973). While several multiplicative agents affected the mortality of winter moths, not all of them contributed to changes in the population size of winter moths.

At least two hypotheses may explain why costs of larval feeding played a minimal role in senita cactus reproduction. First, application of economic theory to mutualism indicates that mutualisms may operate as 'biological markets', in which one species trades commodities or services that it can provide inexpensively (costs) for other commodities or services (benefits) that it cannot produce or affordably obtain (Noe & Hammerstein 1994, 1995; Schwartz & Hoeksema 1998). If mutualisms do operate as biological markets and costs are expressed in demographic currencies, then what are traditionally termed 'costs' to one species may not necessarily reduce that species' reproduction or survival. This is because, under biological market theory, 'costs' are commodities or services that can be produced inexpensively, that is, without significantly affecting a demographic rate. For the senita mutualism, it may be that, because senita cacti produce thousands of flowers and fruit each year, losing a few fruit to larvae does not reduce cactus reproduction.

A second possible hypothesis for why larvae did not reduce reproduction of cacti relates to moth population size and the theory that mutualistic species have mechanisms to limit costs of the interaction (Pellmyr & Huth 1994; Frank 1996; Herre & West 1997; Axén & Pierce

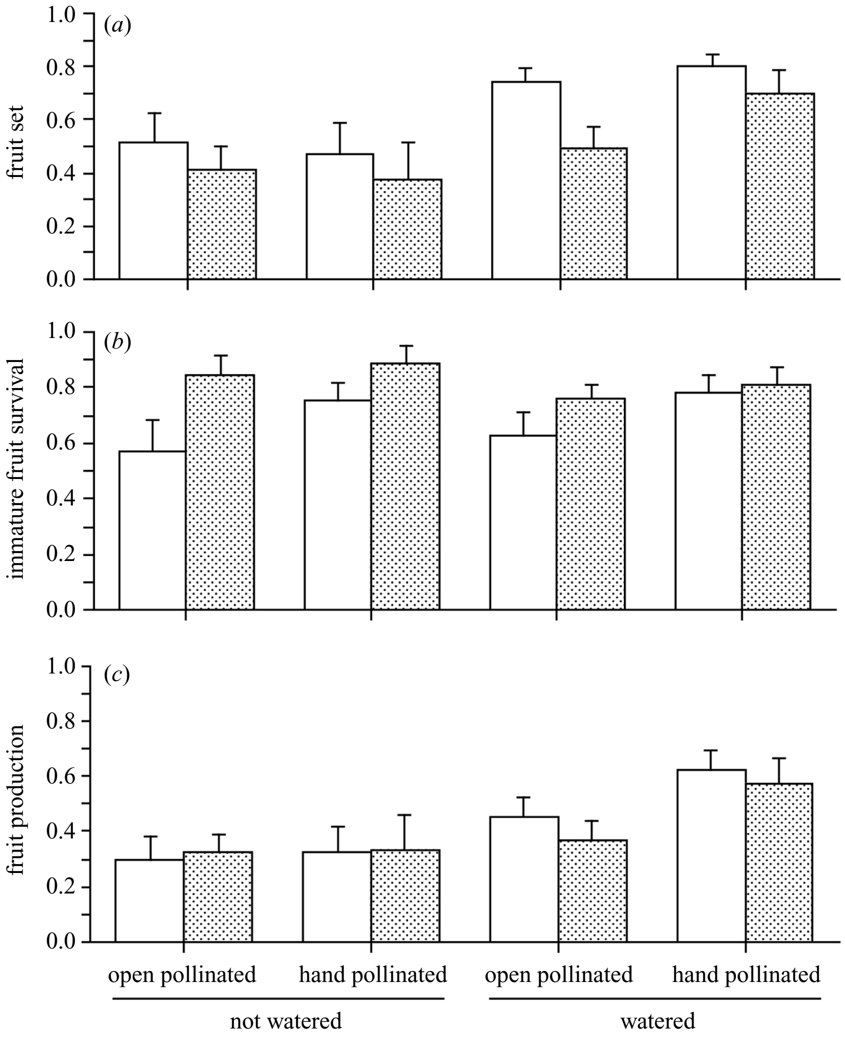

Figure 3. Results of factorial experiment on (*a*) fruit set, the proportion of flowers initiating fruit, (*b*) immature fruit survival, the proportion of initiated fruit producing mature fruit, and (*c*) fruit maturation, the proportion of flowers producing mature fruit. The three treatment factors included water addition (not watered and watered), hand pollinations (open-pollinated and hand-pollinated) and egg removal (eggs intact (open bars) and eggs removed (stippled bars)). Values are means (± 1 s.e.; $n = 5$–7 plants) for each treatment factor.

1998; Yu & Pierce 1998; Herre *et al.* 1999). Clearly, if moths become sufficiently abundant, then enough eggs can be laid to increase larval consumption of fruit and reduce plant reproduction. However, if senita cacti have evolved a mechanism to limit costs by limiting moth abundance, then, in its current ecological and evolutionary state, the cost of fruit consumption may have a minimal effect on demographic rates. When the number of flowers that can set fruit is limited by resource availability, as shown empirically in this study, excess flowers and fruit are aborted. Those eggs and larvae in aborting fruit die. Fruit abortion has been shown in the form of a quantitative model to limit senita moth population size and the costs of larval fruit consumption (Holland & DeAngelis 2001; DeAngelis & Holland 2002; Holland *et al.* 2002). An interesting empirical result predicted by the model was that not only did fruit set increase in the watering experiment but so did flower production, such that rate of fruit abortion remained similar for watered and unwatered plants.

In conclusion, mutualism affects population processes through the effects of benefits and costs on reproduction and survival, but the magnitude of these effects may rest on the demographic effects of factors extrinsic to the interaction. Expressing benefits and costs of mutualism in terms of demographic currencies provides a clear way to study the effects of mutualism on population growth rates and on selection on species traits (this study; Robbins 1991; Hanzawa *et al.* 1988; Schemske & Horvitz 1989). In doing so, this study leads to the hypothesis that extrinsic water limitation and the benefits of pollination are probably more influential than costs of larval feeding for population growth of cacti. Similarly, selection is probably stronger on traits that alleviate water stress and maintain effective pollination than traits associated with costs.

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As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.