



Does having multiple partners weaken the benefits of facultative mutualism? A test with cacti and cactus-tending ants

Tom E. X. Miller

T. E. X. Miller (tmiller2@unl.edu), School of Biological Sciences, Univ. of Nebraska – Lincoln, 348 Manter Hall, Univ. of Nebraska, Lincoln, NE 68588-0118, USA.

Interspecific facultative mutualisms typically involve guilds of interacting species, and species within a guild can vary in the quality of services they provide. For plants that secrete extrafloral nectar (EFN), visitation by multiple ant species that vary in anti-herbivore abilities may result in reduced benefits, relative to an exclusive association with a high-quality mutualist. This raises the intriguing problem of how facultative ant-plant mutualisms persist, given that EFN is costly to produce, yet may confer diminishing returns as partner diversity increases. I tested the prediction that association with two ant partners (*Crematogaster opuntiae* and *Liometopum apiculatum*) weakens benefits to the EFN-producing tree cholla cactus (*Opuntia imbricata*). I found that only one ant (*L. apiculatum*) provided protection against herbivores and seed predators. However, this species associated with cacti more frequently than *Crematogaster* across multiple temporal scales. Within years, *Liometopum* showed greater constancy on plants they occupied, more frequently colonized vacant plants, and replaced but were never replaced by *Crematogaster*. Across years of plant development, *Liometopum* was more abundant on reproductive plants and showed greater overlap with cactus enemies. Simulations of cactus lifetime reproductive output indicated that associating with high- and low-quality mutualists did not significantly reduce plant benefits relative to an exclusive *L. apiculatum* – *O. imbricata* association. The results suggest that non-random interaction frequencies, possibly driven by competition, may contribute to the maintenance of facultative mutualisms involving multiple, qualitatively different partners.

Interspecific facultative mutualisms involve the exchange of non-essential goods or services between members of different species. These can be risky ventures, as variation in the benefits accrued from participation is common and commonly high (Horvitz and Schemske 1990, Rashbrook et al. 1992, Bronstein 1998, Billick and Tonkel 2003, Price et al. 2005). If participation is costly, then any factors that drive benefits below costs could lead to selection against, and the loss of, mutualism traits (Keeler 1981, Rutter and Rausher 2004). Identifying and quantifying sources of variation in benefits are therefore critical steps toward understanding the maintenance or decay of mutually beneficial interactions.

Recent studies have begun to place mutualisms in their community context. Rather than strictly pairwise interactions, mutualisms more often involve guilds of interacting species (Stanton 2003). Furthermore, alter-

nate partner species are often not equally effective, making partner identity an important source of variation in benefits (Horvitz and Schemske 1984, Rico-Gray and Thien 1989, Fraser et al. 2001, Ness et al. 2006). Individuals or species that exploit rewards yet provide few or no benefits impose “missed opportunity costs” on their partner by reducing the frequency with which that partner interacts with other, superior mutualists (Bronstein 2001). Consequently, associating with multiple partners that vary in quality can result in lower net benefits for a focal species compared to an exclusive association with a single effective mutualist (Bronstein et al. 2003, Stanton 2003). This raises the intriguing problem of how generalized, facultative mutualisms persist, given that traits necessary to attract partners may be costly, yet may confer diminishing returns as more partners are recruited and variation in partner quality increases.

Ant visitation to plants that secrete extrafloral nectar (EFN) is a classic example of interspecific facultative mutualism. Ants can have positive effects on EFN-plants by consuming or deterring herbivores. Multiple lines of evidence suggest that EFN is costly for plants to produce (Rutter and Rausher 2004). However, the benefits of EFN production can be highly variable (Bronstein 1998), and ant diversity may be an important component of that variation. Since EFN is a broadly palatable, high quality resource (Carroll and Janzen 1973), EFN-plants typically associate with multiple ant species (Rudgers and Gardener 2004). In addition, numerous studies suggest that alternative ant partners can vary in their capacities for anti-herbivore defense (Horvitz and Schemske 1984, Koptur 1984, Rico-Gray and Thien 1989, Bruna et al. 2004, Mody and Linsenmair 2004, Frederickson 2005, Ness et al. 2006). These patterns suggest that visitation by low-quality ants may lead to a reduction in the frequency of plant interactions with superior species (i.e. missed opportunity costs) and, consequently, a reduction in benefits (Fraser et al. 2001, Raine et al. 2004, Frederickson 2005). However, plants may not require biotic defense at all points in time and space, and missed opportunities to interact with superior bodyguards are only costly when they coincide with enemy attack. Thus, the temporal dynamics of both plant-partner associations and herbivore pressure are likely to be critical determinants of the net benefits of EFN production.

An important component of the temporal dynamics of mutualism is turnover in partner identity. Turnover has been observed in ant protection interactions on the scales of hours to months (Horvitz and Schemske 1990, Alonso 1998, Oliveira et al. 1999, Fraser et al. 2001). The degree and direction of turnover are likely to influence individual plant benefits, which should be maximized when superior bodyguards exhibit greater temporal constancy than other, inferior species in the mutualist guild. Conversely, a negative correlation between mutualist quality and temporal constancy may exacerbate missed opportunity costs and weaken plant benefits.

Turnover in partner identity can also occur in relation to plant ontogeny (Fonseca and Benson 2003). Susceptibility to enemies can change dramatically throughout plant development (Fenner et al. 1999, Warner and Cushman 2002, Boege and Marquis 2005), suggesting that plant defense traits, including biotic defense, should also be stage-dependent. Yet, we know little about ontogenetic variation in ant abundance or identity on EFN-plants (Di Giusto et al. 2001, del-Val and Dirzo 2003, Fonseca and Benson 2003). Like short-term constancy, plant stage-related variation in partner identity should influence the long-term benefits of the interaction since those species at highest

frequency on the most susceptible stages will have differential effects on plant lifetime fitness.

I studied the EFN-bearing tree cholla cactus (*Opuntia imbricata*) and its two ant visitors, *Crematogaster opuntiae* and *Liometopum apiculatum*. Previous studies of EFN-bearing cacti have demonstrated net positive effects of ant visitation (Pickett and Clark 1979, Oliveira et al. 1999), but the effect of ant diversity on the magnitude of benefits is relatively unexplored (Ness et al. 2006). Furthermore, this study system is particularly appropriate for questions about the maintenance of facultative mutualism. The genus *Opuntia* contains species that do and do not secrete EFN (Kathleen H. Keeler and T.E.X. Miller, unpubl.), suggesting that mutualism traits in this group are evolutionarily labile and may be lost if their benefits are not consistently high.

The goals of this study were to test the prediction that having multiple partners weakens the benefits of mutualism for an EFN-plant, relative to an exclusive association with a high-quality partner, and to explore how the temporal dynamics of plant-partner associations influence the effects of ant diversity on plant benefits. I used a combination of observational and experimental field data spanning three years to address the following questions: (1) do ant species differ in their abilities to defend cacti against enemies? (2) Do ant species differ in temporal constancy on individual plants within a season? (3) Do the distributions of ants and herbivore pressure vary across years and stages of plant development? Finally, I used these field data to construct simulation models that explored the consequences of having multiple partners for plant lifetime benefits.

Methods

Study system

This study was conducted in the Los Pinos mountains, a small mountain chain located on the Sevilleta National Wildlife Refuge, a Long-term Ecological Research (LTER) site in central New Mexico (34°20'5.3"N, 106°37'53.2"W). The habitat is characterized by steep slopes, rocky soils, and abundant perennial vegetation including cactus, yucca, oak, and juniper.

Tree cholla cacti (*Opuntia imbricata*) are common in high Chihuahuan desert habitats (Benson 1982). Tree cholla is an arborescent cactus with cylindrical stem segments and large, conspicuous spines. It is native to the southwestern US and common throughout New Mexico, southern Colorado, and southwest Texas (Fraser and Pieper 1972). Plants initiate new stem segments and flower primordia from specialized axillary

buds at the terminal ends of stem segments. In central New Mexico, vegetative growth occurs from May – August, and flowering occurs throughout June and July.

Tree cholla cacti secrete nectar from specialized glands on young vegetative and reproductive structures. Like other EFN-bearing cacti, tree cholla does not secrete nectar from older plant parts (Oliveira et al. 1999, Ness et al. 2006). At the Sevilleta, tree cholla cacti are visited primarily by two ground-nesting ant species: *Crematogaster opuntiae* and *Liometopum apiculatum*. These species never co-occur on the same plant, which is generally interpreted as evidence for competition among ants for plant services (Horvitz and Schemske 1990, Heil et al. 2001, Bruna et al. 2004, Morris et al. 2005, Ness et al. 2006). Since an individual plant does not interact with both species simultaneously, my use of the term “multiple partners” refers to interactions over a plant’s lifetime. I occasionally observed other ant species on tree cholla during this study, but at very low frequency.

A variety of insect herbivores and seed predators attack tree cholla throughout its range (Mann 1969, 1970). There were three plant enemies that commonly occurred at the Sevilleta during this study. These included an unidentified weevil of the genus *Gerstaeckeria*, which feed externally on both vegetative and reproductive structures as adults, and overwinter as larvae within the plant. Another common herbivore, the cactus bug, *Narnia pallidicornis* (Hemiptera: Coreidae), feeds on all cactus parts but prefer reproductive structures (Miller et al. 2006). Finally, developing fruits were attacked by the pre-dispersal seed predator *Cabela ponderosella* (Lepidoptera: Pyralidae). These moths oviposit in open cactus flowers in June or July, and larvae burrow into the ripening ovary.

Census data collection

I quantified insect abundance and herbivore damage on marked tree cholla across the 2004 and 2005 growing seasons. These censuses included 40 plants located in each of three spatial blocks, separated by approximately 2 km, for a total of 120 plants. The sample population within each block was randomly selected, but stratified to include 10 small (<0.5 m tall, juvenile), 10 medium (>0.5 m tall, juvenile), and 20 large (>1 m, reproductive) plants. In both years, all plants were visited during three census periods: early-season (24 May–4 June 2004, 26 May–9 June 2005), mid-season (16–26 July 2004, 3–8 July 2005 for adults and 24–28 July 2005 for juveniles), and late-season (12 August–2 September 2004, 2–12 September 2005). Additionally, 20 large plants in one of the blocks were visited three times in 2003 (2–4 June, 11–12 July and 17–18 August). For all plants on each date,

I recorded herbivore and seed predator abundances, identified the ant species present (*Crematogaster* or *Liometopum*), and quantified the abundance of each species by counting as many ants as I could locate in 30 s.

For large plants, I estimated herbivore damage to vegetative parts by randomly selecting two “clusters” of newly produced stem segments. I counted the number of segments in each cluster, and counted the number of damage marks on all segments in the cluster. Damage included bite marks left by weevils, chlorotic marks left by cactus bugs, and signs of internal damage by weevil larvae. I quantified vegetative damage for each plant as the number of damage marks per stem segment, averaged over two stem segment clusters. Damage data were collected during the late-season census period, and represented the maximum damage per plant within a season. I also quantified pre-dispersal seed predation as the proportion of total fruits at the mid-season census occupied by a *Cabela* larva. Larval entrance into the fruit leaves a distinctive scar (Mann 1969, Pickett and Clark 1979), which allowed me to score presence or absence unambiguously.

Tree cholla grows modularly, each year adding new stem segments to the terminal ends of segments produced the previous year. This growth habit allowed me estimate age for each of the census plants by counting stem segments from the most recent growth to the root crown. I also calculated the average age at which cacti began to reproduce by taking the mean age in 2005 of plants that reproduced in 2005 but did not reproduce in 2004 ($n=40$). I focus on plant age because it conveniently links size, developmental stage and time.

Ant exclusion experiment

I conducted an experiment to ask if *Crematogaster* and *Liometopum* differed in their abilities to protect cacti from enemies. Because both ant species are ground-nesting, randomly assigning partner identity to plants would have been very difficult, and such treatment assignments might not have been retained because of species turnover (Results). For these reasons, I instead compared herbivore damage among plants with all ants experimentally excluded, unmanipulated plants occupied by *Crematogaster*, and unmanipulated plants occupied by *Liometopum*. This experiment was embedded (spatially and temporally) within the census blocks described above, allowing me to make direct comparisons between experimental and census plants. In early May 2005, I randomly selected 10 additional, large cacti in each of the three blocks. Within each block, five plants were assigned to complete ant exclusion, and five plants were unmanipulated.

For plants assigned to ant exclusion, I carefully applied the non-systemic insecticide Carbaryl (1-naphthyl N-methylbarbamate; commercial name: Sevin) around the trunk near the base of the plant. The insecticide was diluted to 0.04 fl. oz. active ingredient per gallon H₂O, which is 1/8 the concentration recommended by the manufacturer for deterring herbivores. This protocol was effective at excluding ants (mean $\pm$ SE abundance on exclusion plants: 7.5 ± 3.5 ants, control plants: 28.0 ± 5.5 ants [$t = 3.17$, $p = 0.0038$, $n = 15$]). Neither the insecticide nor the addition of water had any effects on the plants (Miller 2007), and this treatment had no obvious negative effects on cactus herbivores (herbivory was greatest on ant exclusion plants; Results). I applied insecticide five times (22 May, 18 June, 2 July, 4 August, 29 August) to maintain the ant exclusion treatment throughout the season. I visited all plants three times during summer 2005, and these dates coincided with the early-, mid-, and late-season census periods. For each plant, I recorded the abundances of each ant species, and I quantified damage and pre-dispersal seed predation as above.

For analysis, I combined data from the 30 experimental plants with the 2005 data from the 60 large census plants. I removed from the analysis all plants without ants, or with turnover in ant identity. I then sorted this data set into three treatments: ant exclusion ($n = 15$), *Crematogaster* ($n = 13$), and *Liometopum* ($n = 41$). *Crematogaster* were rare and *Liometopum* were common on large plants (Results) which made this data set highly unbalanced. Before analyzing the full data set, I ran simulations using Visual Basic in Microsoft Excel to ask if the greater sample size for the *Liometopum* group would influence comparisons to the treatment groups with smaller sample sizes. I found that the means of small ($n = 13$) random samples drawn from the complete *Liometopum* data ($n = 41$) were significantly different from the mean of the full data set in fewer than 5% of 1000 iterations for each response variable. I concluded that use of the full *Liometopum* data set was appropriate.

I used ANOVA to analyze the effects of ant treatment (fixed) and spatial block (random) on two dependent variables: vegetative damage and pre-dispersal seed predation. I square root- and arcsin square root-transformed the vegetative damage and seed predation data, respectively. Visual inspection of residuals indicated that ANOVA assumptions were met. For models that were statistically significant, I performed two pre-planned contrasts to ask if each species provided benefits to cacti: *Crematogaster* vs ant exclusion, and *Liometopum* vs ant exclusion.

An important limitation of this experimental design is that, because ant species were not randomly assigned to plants, partner identity may be confounded with

other plant traits that influence herbivory. To evaluate this possibility, I compared multiple size- and performance-related plant traits between *Liometopum*- and *Crematogaster*-tended plants using a multivariate analysis of variance (MANOVA). These traits were: size, age, number of new stem segments produced, number of flower buds produced, and vegetative growth. Size was estimated as cylindrical volume (cm³) using height and width measurements. Growth was calculated as the mean length of all newly produced stem segments on two randomly selected clusters on each plant in September, when segment elongation was complete. I examined each variable for normality and equality of variances and found that no transformations were necessary.

Turnover in ant species occupancy

I used the census data to quantify within-season turnover in ant species occupancy and identity. For each within-season transition (early- to mid-season and mid- to late-season) in each year (2003, 2004, 2005), I created a 3×3 matrix in which columns denote the state of ant occupancy (*Crematogaster*, *Liometopum*, or vacant) at time t , rows denote the state at $t + 1$, and cell entries are frequencies of observed transitions. The time interval was approximately two months. In preliminary observations, no turnover occurred during shorter (two week) intervals, and so any turnover that occurred between these censuses was likely minimal. I used a log-linear analysis to examine the effects of time of season, year, and season $\times$ year interaction on transition frequencies.

Distributions of ants and herbivores across plant stages

I used the census data to ask if *Crematogaster* and *Liometopum* differ in their distributions across plant ages and stages. I also examined the distribution of herbivore pressure, and compared ant and herbivore data to ask if either ant species shows greater overlap with plant enemies over the course of plant development. I sorted all plants by age, which ranged from 2 to 18 yr. Plants < 5 or > 13 yr were lumped to ensure adequate sample sizes at the ends of the age distribution. Samples sizes for each age ranged from $n = 7$ to $n = 15$.

I examined ant distributions across plant stages in two ways. First, I analyzed the probability of ant presence and identity with logistic regressions. In one logistic regression, I modeled the probability of occupancy by ants, irrespective of species, as a function of cactus age. In a second logistic regression, I modeled, for occupied plants, the probability of being occupied by *Liometopum* vs

Crematogaster as a function of cactus age. Second, I calculated the mean abundance of each ant species for plants of each age (excluding unoccupied plants). I also split the data set into two groups based on plant reproductive status: juvenile (< mean age at onset of reproduction; n = 44) and reproductive (≥ mean age at reproduction; n = 55). I examined the effects of reproductive status and ant identity on square root-transformed ant abundance using a two-way ANOVA.

To examine variation in herbivore pressure throughout plant development, I calculated the total number of insect herbivores (weevils, bugs, moths) on plants of each age. Because older plants may support more insects simply because they are larger, I standardized these counts by dividing insect totals by the number of new plant structures (fruits and stem segments), which are the primary resources for cactus herbivores (Mann 1969, 1970) and are correlated with plant size (unpubl.). While different herbivore species may not inflict equal amounts or types of damage, this index gives a broad estimate of susceptibility to the entire guild of enemies. As above, I split the herbivore data according to plant reproductive status, and compared juvenile and adult plants using a t-test.

Simulations of lifetime benefits of ant visitation

Finally, I used these data and other empirical estimates of plant performance and enemy impacts to simulate lifetime seed production under different scenarios of ant visitation, and to explore the consequences of partner diversity for the benefits of mutualism. I briefly

describe the models here and provide additional information, including parameter values and equations, in Appendix 1.

These were individual-based stochastic simulation models, and the output of interest was cumulative seed production over a 20-year cactus lifespan (Kunst 1990). Time was included explicitly in the models to reflect partner variation and turnover as it occurs in nature (Results). The simulations consisted of five steps that occurred within each year of a plant’s lifetime, described in Fig. 1. I constructed six models based on this sequence. One model (“Liom.>Crem.”) represented the actual state of the system, with *Liometopum* showing greater within-season constancy and more frequently occupying older plants than *Crematogaster* (Results). The other models considered hypothetical scenarios in which interaction frequencies were equal (“Liom.=Crem.”), biased toward *Crematogaster* (“Crem.>Liom.”), only one ant species occurred (“Liom. only”, “Crem. only”), or no ants occurred (“no ants”). For the two-species models, I use inequality symbols to denote the relative probabilities of species occurrence on an individual plant, within and across years (step 1 and 3).

The effect of moth larvae on seed production was estimated by comparing seed counts from infested fruits with predictions based on a regression of seed number vs. fruit mass for non-infested fruits (Appendix 1). Each simulation was iterated 10 000 times, and parameter values were re-drawn from their respective distributions in each year of each iteration. I used ANOVA and Bonferroni-adjusted LSD tests to

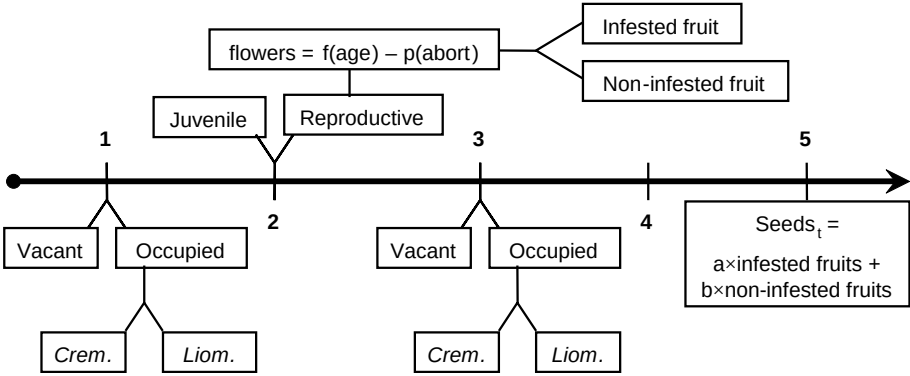


Fig. 1. Sequence of individual-based stochastic simulations of cactus lifetime reproductive output. These five steps occur in each year (t) of a plant’s lifetime. Branched lines represent mutually exclusive alternatives. 1) At the start of each growing season, a plant was identified as vacant or occupied, and occupied plants were assigned an ant species; ant status at step one was dependent upon plant age. 2) Plants were identified as either juvenile or reproductive according to age, and the number of flowers produced by reproductive plants was equal to age-dependent fecundity minus some proportions of flower buds that were aborted. 3) At mid-season, ant occupancy and identity were re-assigned; ant status at this step depended on early-season occupancy and identity. 4) For reproductive plants, mid-season ant status determined the proportion of developing fruits that was attacked by seed-eating moth larvae. 5) Total seed production in year t of a plant’s life was tallied combining seed production from uninfested and infested fruits.

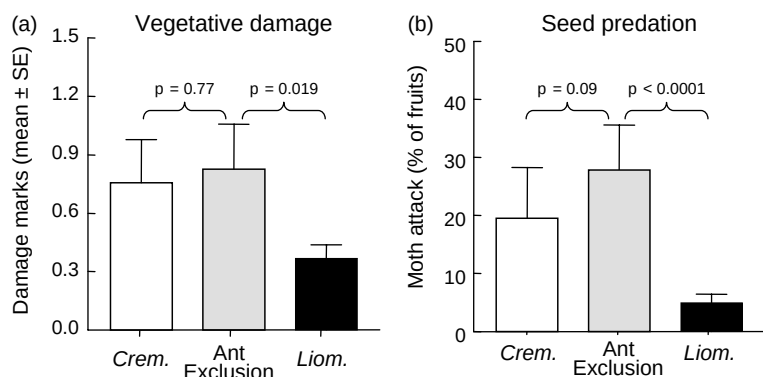


Fig. 2. Benefits conferred by two cactus-tending ants. Plants in the ant exclusion group received dilute applications of insecticide, and plants in the Crem. and Liom. groups were visited exclusively by *Crematogaster opuntiae* and *Liometopum apiculatum*, respectively. (a) Damage marks by insect herbivores to vegetative structures, and (b) percentage of fruits infested by seed-feeding moth larvae. Results of pre-planned contrasts (each species vs ant exclusion) are shown for statistically significant univariate ANOVA's ($\alpha = 0.05$). Bars represent standard errors.

compare lifetime seed production among the six simulations. Comparing “Liom. > Crem.” with “Liom. only” allowed me to ask if plant benefits under observed conditions are significantly lower than would be expected if the superior mutualist was the sole partner. The additional two-ant simulations allowed to me explore the consequences of different interaction frequencies.

Results

Ant exclusion experiment

Plants with ants experimentally excluded and plants tended by *Crematogaster* experienced significantly greater herbivore damage to vegetative structures than plants tended by *Liometopum* (Fig. 2a; $F_{2,71} = 3.98$, $p = 0.023$). Rates of attack by seed-eating moth larvae showed the same pattern ($F_{2,65} = 9.89$, $p = 0.0002$; Fig. 2b). MANOVA results indicated that plants occupied by *Liometopum* and *Crematogaster* were statistically identical in age, size, flower and segment

production, and vegetative growth rate (Wilk's $\Lambda = 0.929$, $F_{5,42} = 0.64$, $p = 0.67$).

Turnover in ant species occupancy

Crematogaster and *Liometopum* showed very different patterns of temporal constancy and turnover on individual plants within a growing season. Log-linear analysis revealed no significant differences in transition frequencies among years or between early- and late-season (year: $\chi^2 = 2.71$, $p = 0.099$; season: $\chi^2 = 0.68$, $p = 0.41$; year $\times$ season: $\chi^2 = 0.41$, $p = 0.52$), and so I present the pooled matrix (Table 1, $n = 520$ observed transitions). For plants occupied by *Crematogaster* at time t , only about half were still occupied by this species at the next census. By contrast, 78% of plants with *Liometopum* were still occupied by this species at the next census. *Liometopum* more frequently colonized vacant plants than *Crematogaster* (0.22 vs 0.09). In addition, *Crematogaster* was sometimes replaced by *Liometopum* during a census period, but the reverse never occurred (0.14 vs 0) across 9 censuses over 3 years.

Table 1. Within-season turnover in ant occupancy on tree cholla cacti. Columns represent each of three possible ant occupancy states (*Crematogaster*, *Liometopum*, or vacant) at time t , and entries within columns indicate the proportion of plants classified in each state at time $t+1$. Transitions from t to $t+1$ represent early-to-mid-season and mid-to-late-season transitions over three years ($n = 520$ transitions). Observed transitions from all states at time t were significantly different from random expectation (*Crematogaster*: $\chi^2 = 16.33$, $p = 0.003$; *Liometopum*: $\chi^2 = 232.8$, $p < 0.0001$; vacant: $\chi^2 = 118.3$, $p < 0.0001$).

		Ant occupancy (t)		
		Crem.	Liom.	Vacant
Ant occupancy ($t+1$)	Crem.	0.53	0.00	0.09
	Liom.	0.14	0.78	0.22
	Vacant	0.33	0.22	0.69

Distributions of ants and herbivores across plant stages

Logistic regression analyses indicated that both ant presence and ant identity were plant age-dependent (Fig. 3). The probability of a cactus being occupied by any ant increased with plant age (Fig. 3a; Likelihood ratio test of $\beta = 0$: $\chi^2 = 20.9$, $p < 0.0001$). For occupied plants, the probabilities of being occupied by either *Crematogaster* or *Liometopum* were roughly equal for young plants but *Liometopum* was the more likely occupant on older plants (Fig. 3b; Likelihood ratio test of $\beta = 0$: $\chi^2 = 5.91$, $p = 0.015$).

Analyses of abundance were consistent with the logistic regression results, and indicated that the shift in partner identity coincided with the onset of plant reproduction (mean $\pm$ SE age at reproduction: 8.8 ± 0.29 yr). *Crematogaster* and *Liometopum* were similarly

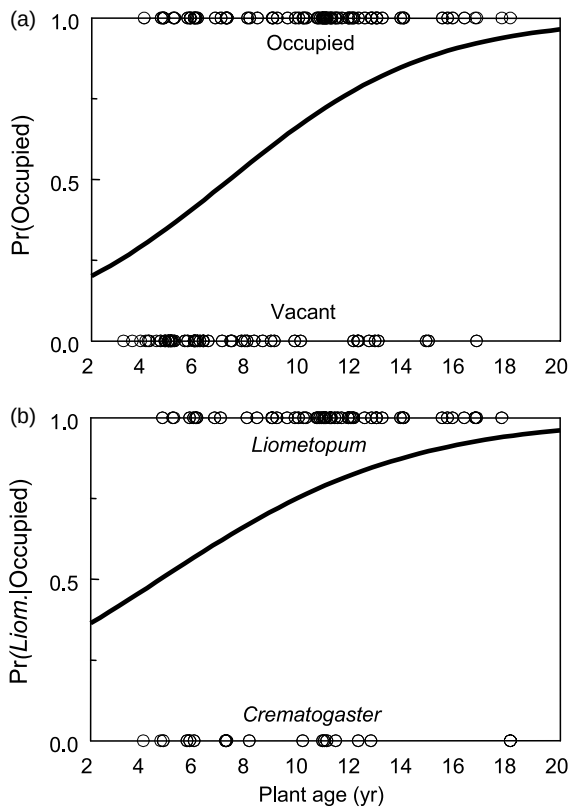


Fig. 3. Logistic regression models of ant presence and identity as functions of plant age. (a) Probability of occupancy; circles represent plants that were either vacant or occupied, and solid line is the fitted logistic model for the probability of occupancy. (b) Probability of ant identity, given occupancy; circles represent plants occupied by either *Crematogaster* or *Liometopum*, and solid line is the fitted logistic model for the probability of *Liometopum*. Circles are jittered along the horizontal axes to show multiple plants of the same age.

abundant on juvenile plants, but *Liometopum* was more abundant on older, reproductive plants (Fig. 4a), as indicated by a significant species $\times$ stage interaction ($F_{1,236} = 13.45$, $p = 0.0003$). *Liometopum* showed greater overlap across stages with plant enemies. Herbivore pressure was significantly greater on older plants compared to juveniles ($t = -3.7$, $p = 0.0003$; Fig. 4b). This was driven, in part, by the fact that seed-eating moth larvae were only found on reproductive plants.

Simulations of lifetime benefits of ant visitation

Partner identity and diversity had significant effects on model-generated estimates of cactus lifetime reproductive success (Fig. 5; $F_{5,6E4} = 44.08$, $p < 0.0001$). Lifetime seed production under current, observed conditions of ant visitation (Liom. > Crem.) is represented by the black bar in Fig. 5, and other hypothetical scenarios are represented by white bars. All simulations that included ants resulted in significantly greater seed production compared to the no-ant scenario. Simulated plants visited exclusively by *Liometopum* produced more seeds over their lifetimes than either plants visited exclusively by *Crematogaster* or plants visited by both species, consistent with the prediction that having multiple partners weakens benefits. However, the degree to which associating with both *Crematogaster* and *Liometopum* reduced plant benefits (relative to the *Liometopum*-only scenario) varied across simulations and depended upon relative interaction frequencies. Estimates of reproductive output under observed conditions (Liom. > Crem.) were only slightly, and not significantly less than estimates from the *Liometopum*-only scenario. In contrast, simulations in which the two species interacted with cacti with equal probabilities (Liom. = Crem.) or where interaction frequencies were biased toward the inferior mutualist (Crem. > Liom.) resulted in estimates of seed production significantly lower than both the *Liometopum*-only and observed scenarios.

Discussion

Partner-specific biotic defense

The two ant species that visited tree cholla extrafloral nectaries were not equally effective mutualists. *Liometopum apiculatum* provided biotic defense against herbivores that fed on vegetative plant parts (Fig. 2a) and against seed-eating moth larvae that attacked cactus fruits (Fig. 2b). *Crematogaster opuntiae*, in contrast, provided no defense against vegetative herbivores nor against seed predators. The finding that *Crematogaster*- and *Liometopum*-tended plants do not differ in any of

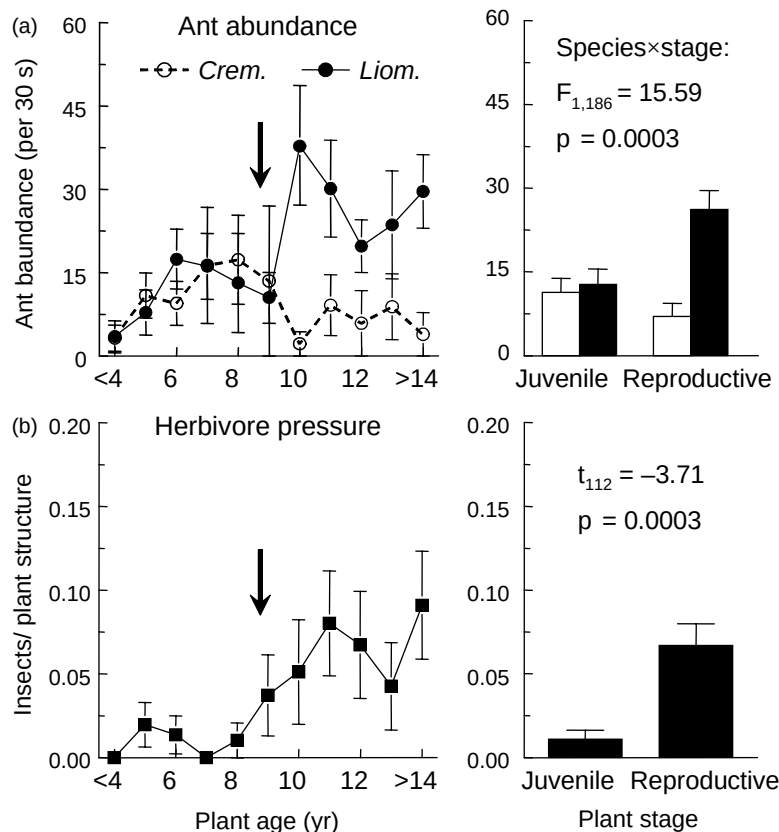


Fig. 4. Plant age-related variation in mutualism and herbivory. (a) Abundances of *Crematogaster* and *Liometopum* on tree cholla. Points are mean abundances per age and bars in the right panel show mean abundances of *Crematogaster* (open bars) and *Liometopum* (filled bars) pooled across juvenile (<9 yr) and reproductive (≥ 9 yr) plants. (b) Herbivore pressure (insect abundance per resource structure). Points show mean abundances per age and bars are pooled across juvenile and reproductive plants. Arrows indicate the average plant age at the onset of reproduction. All error bars show standard errors.

the size or performance traits I measured supports the interpretation that these ant species differ in their protective abilities, as opposed to plant or microhabitat influences on herbivory. Pickett and Clark (1979) studied the interactions among *Crematogaster opuntiae*, a different EFN-secreting cactus species (*Opuntia acanthocarpa*), and a different herbivore (*Chelinidea vittiger* [Hemiptera: Coreidae]) in a different habitat (Sonoran desert). Interestingly, they concluded that this ant species was a highly effective bodyguard. The discrepancy between my results and theirs illustrates the widely held view that the outcomes of ant–plant interactions are highly conditional and subject to multiple sources of variation, including species effects (Bronstein 1998) and abiotic context (Kersch and Fonseca 2005).

The experimental results support previous findings that different ant species can vary in the benefits they confer to a common plant partner (Horvitz and Schemske 1984, Rico-Gray and Thien 1989, Fraser et al. 2001, Bruna et al. 2004, Mody and Linsenmair

2004, Frederickson 2005). The differences in anti-enemy ability suggest that visitation by *Crematogaster* may represent missed opportunities for cacti to associate with *Liometopum*, the superior bodyguard. However, I also found non-random temporal patterns of interaction between cacti and each ant species, which mediated the negative effects of associating with multiple ant partners.

Temporal variation in ant occupancy and identity

Tree cholla of all ages produced EFN, but the probability that a plant was occupied by any ant increased with age (Fig. 3a). Active extrafloral nectaries on tree cholla are restricted to young vegetative and reproductive parts. Total plant structures (and therefore total nectar availability) increases with age, making older plants better resources for ants than younger ones. In addition, the production of reproductive structures by older plants may increase the quantity and/or quality

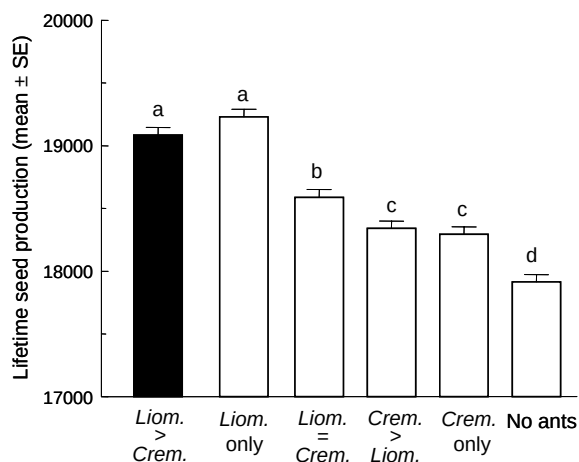


Fig. 5. Simulations of tree cholla lifetime reproductive output under different scenarios of ant visitation. Simulated cacti were visited by either two, one, or no ant species over 20 years. In the 2-species simulations, equality symbols refer to relative interaction frequencies. The black bar represents the actual state of the system based on empirical results and white bars are hypothetical scenarios. Letters above bars indicate statistical differences based on multiple comparisons with adjusted p-values.

of rewards they provide to ant partners. The onset of plant reproduction (at about 9 yr) coincided with greater probabilities of occupancy (Fig. 3a) and greater overall ant abundance (Fig. 4a). Optimal defense theory (ODT; Rhoades 1979) predicts that plant defenses should be preferentially allocated toward structures that confer the greatest fitness benefits. Empirical tests of ODT have generally found that reproductive structures are better chemically defended than vegetative structures (Zangerl and Bazzaz 1992, Zangerl and Rutledge 1996, Karban and Baldwin 1997). In one of the few applications of ODT to biotic defense, Wäckers and Bonifay (2004) found that EFN production from the bracteal nectaries of cotton plants (*Gossypium hirsutum*) exceeded that of foliar nectaries. My results are also consistent with ODT and suggest that the production of reproductive structures increases ant recruitment at the whole-plant level.

For occupied plants, partner identity varied through time. *Crematogaster* and *Liometopum* differed in rates of within-season turnover, tracked over three years. *Liometopum* showed greater constancy on plants they occupied, more frequently colonized vacant plants, and replaced but were never replaced by *Crematogaster* (Table 1). I also observed replacement across years of plant development. Young plants had equal probabilities of occurrence (Fig. 3b) and similar abundances (Fig. 4a) of *Crematogaster* and *Liometopum*. However, *Liometopum* was more likely and more abundant than *Crematogaster* on older plants, and the shift in partner

identity coincided with the onset of plant reproduction (Fig. 4a). Pressure from herbivores and seed predators also varied across plant stages, with mature, reproductive plants being more susceptible to attack than juveniles (Fig. 4b). Thus, *Liometopum*, the better bodyguard, also showed greater overlap with plant enemies, both within a season and across years of plant development.

Does having multiple partners weaken benefits?

Simulation models indicated that the temporal variation in partner identity I observed directly influenced the consequences of visitation by multiple ant species over the plant's lifetime. The most important insight provided by the simulation approach is that interactions with both *Crematogaster* and *Liometopum* led to weak and non-significant reductions in plant benefits (lifetime seed production) compared to an exclusive *Liometopum*-cactus association (compare "Liom. > Crem." and "Liom. only" in Fig. 5). However, simulations of hypothetical scenarios in which the two species occurred on plants with equal probabilities, or where interaction frequencies were biased toward *Crematogaster* resulted in significant reductions in plant lifetime benefits.

The patterns of change in ant identity, combined with the lack of co-occurrence on individual plants, suggest that these two species compete for plant services (especially high-quality, reproductive plants), and that *Liometopum* is the superior competitor. In this light, my results support Stanton's (2003) prediction that competition within a mutualist guild could influence the magnitude of benefits received by a shared partner. However, this study did not explicitly test for competitive interactions between *Liometopum* and *Crematogaster*, and it is possible that other or additional mechanisms drive variation in partner identity.

Ant-plant studies rarely examine variation in partner abundance or identity over multiple plant life stages. The results of this study clearly indicate that ontogenetic variation is a critical determinant of plant lifetime benefits. In addition, these patterns may also have important community-level consequences. Plant size-related variation in the identities of ant occupants has been documented for a handful of obligate myrmecophytes (plants whose domatia are inhabited by ant colonies), and these authors concluded that "ontogenetic succession" (Fonseca and Benson 2003) in occupancy may facilitate the coexistence of competitors within ant communities (Davidson et al. 1989, Young et al. 1997, Vasconcelos and Davidson 2000, Fonseca and Benson 2003). Despite its potential importance for the evolutionary and community ecology of ant-plant interactions, the generality of partner

succession over the course of plant development is unknown. The role of plant ontogeny in maintaining the coexistence of *Crematogaster* and *Liometopum* war-rants further study.

In summary, these results demonstrate the importance of the temporal dynamics of ant-plant associations for determining the effects of partner diversity on plant benefits. Under certain conditions, plants can retain relatively high benefits of EFN production despite associating with high- and low-quality ant partners. Since EFN production is likely to be costly (Agrawal and Rutter 1998, Rudgers and Gardener 2004, Rutter and Rausher 2004), these results further suggest that any processes that influence the relative frequencies of alternative associations – such as competitive interactions among partners – could facilitate the maintenance, or accelerate the decay, of facultative mutualism through their effects on net benefits and cost-benefit ratios. Studies that quantify both costs and benefits in a common currency are needed to test this and other hypotheses about the evolutionary trajectories of facultative mutualisms.

Acknowledgements – I am grateful to the Sevilleta community (LTER and US Fish and Wildlife Service) for providing a stimulating research environment and logistical support. Jeremiah Dye identified ants and Massa Takahashi identified herbivores. Judie Bronstein and Eben Gering provided helpful discussion and Jim Eckberg, Diana Pilson, Holly Prendeville, Tomomi Suwa and Brigitte Tenhumberg offered insightful comments that improved this manuscript. Financial support for this work came from the Initiative for Ecological and Evolutionary Analysis at the Univ. of Nebraska – Lincoln, the School of Biological Sciences' Blair Paxton fund (UN-L), the Sevilleta LTER (NSF DEB-0217774), and a Graduate Assistance in Areas of National Need (GAANN) fellowship. Finally, I am indebted to John Mann, whose monograph inspired my interest in cactus insects.

References

- Agrawal, A. A. and Rutter, M. T. 1998. Dynamic anti-herbivore defense in ant-plants: the role of induced responses. – *Oikos* 83: 227–236.
- Alonso, L. E. 1998. Spatial and temporal variation in the ant occupants of a facultative ant-plant. – *Biotropica* 30: 201–213.
- Benson, L. 1982. *Cacti of the United States and Mexico*. – Stanford Univ. Press.
- Billick, I. and Tonkel, K. 2003. The relative importance of spatial vs temporal variability in generating a conditional mutualism. – *Ecology* 84: 289–295.
- Boege, K. and Marquis, R. J. 2005. Facing herbivory as you grow up: the ontogeny of resistance in plants. – *Trends Ecol. Evol.* 20: 441–448.
- Bronstein, J. L. 1998. The contribution of ant-plant protection studies to our understanding of mutualism. – *Biotropica* 30: 150–161.
- Bronstein, J. L. 2001. The exploitation of mutualisms. – *Ecol. Lett.* 4: 277–287.
- Bronstein, J. L. et al. 2003. Ecological dynamics of mutualist/antagonist communities. – *Am. Nat.* 162: S24–S39.
- Bruna, E. M. et al. 2004. Interspecific variation in the defensive responses of obligate plant-ants: experimental tests and consequences for herbivory. – *Oecologia* 138: 558–565.
- Carroll, C. R. and Janzen, D. H. 1973. Ecology of foraging ants. – *Annu. Rev. Ecol. Syst.* 4: 231–257.
- Davidson, D. W. et al. 1989. Competition among ants for myrmecophytes and the significance of plant trichomes. – *Biotropica* 21: 64–73.
- del Val, E. and Dirzo, R. 2003. Does ontogeny cause changes in the defensive strategies of the myrmecophyte *Cecropia peltata*? – *Plant Ecol.* 169: 35–41.
- Di Giusto, B. et al. 2001. Variation in the effectiveness of biotic defence: the case of opportunistic ant-plant protection mutualism. – *Oecologia (Berlin)* 129: 367–375.
- Fenner, M. et al. 1999. Comparison of seedling and adult palatability in annual and perennial plants. – *Funct. Ecol.* 13: 546–551.
- Fonseca, C. R. and Benson, W. W. 2003. Ontogenetic succession in Amazonian ant tress. – *Oikos* 102: 407–412.
- Fraser, A. M. et al. 2001. Assessing the quality of different ant species as partners of a myrmecophilous butterfly. – *Oecologia* 129: 452–460.
- Fraser, J. G. and Pieper, R. D. 1972. Growth characteristics of *Opuntia imbricata* (Haw.) D.C. in New Mexico. – *Southwest Nat.* 17: 229–237.
- Frederickson, M. E. 2005. Ant species confer different partner benefits on two neotropical myrmecophytes. – *Oecologia* 143: 387–395.
- Heil, M. et al. 2001. On the benefits of indirect defense: short- and long-term studies of antiherbivore protection via mutualistic ants. – *Oecologia* 126: 395–403.
- Horvitz, C. C. and Schemske, D. W. 1984. Variation among floral visitors in pollination ability: a precondition for mutualism. – *Science* 225: 519–521.
- Horvitz, C. C. and Schemske, D. W. 1990. Spatiotemporal variation in insect mutualists of a neotropical herb. – *Ecology* 71: 1085–1097.
- Karban, R. and Baldwin, I. T. 1997. *Induced response to herbivory*. – Univ. of Chicago Press.
- Keeler, K. H. 1981. A model of selection for facultative, nonsymbiotic mutualism. – *Am. Nat.* 118: 488–498.
- Kersch, M. F. and Fonseca, C. R. 2005. Abiotic factors and the conditional outcome of an ant-plant mutualism. – *Ecology* 86: 2117–2126.
- Koptur, S. 1984. Experimental evidence for defense of *Inga* (Mimosoideae) saplings by ants. – *Ecology* 65: 1787–1793.
- Kunst, C. R. G. 1990. Some autecological aspects of *Opuntia imbricata* (Haw.) D.C. (Cholla). – PhD thesis. Texas Tech Univ.

- Mann, J. 1969. Cactus-feeding insects and mites. – Smithsonian Inst.
- Mann, J. 1970. Cacti naturalized in Australia and their control. – Government Printer, Brisbane.
- Miller, T. E. X. 2007. Spatial and temporal dynamics of interacting populations: cacti and cactus-feeding insects in the Chihuahuan desert. – PhD thesis, Univ. of Nebraska-Lincoln.
- Miller, T. E. X. et al. 2006. Plant reproductive allocation predicts herbivore dynamics across spatial and temporal scales. – *Am. Nat.* 168: 608–616.
- Mody, K. and Linsenmair, K. E. 2004. Plant-attracted ants affect arthropod community structure but not necessarily herbivory. – *Ecol. Entomol.* 29: 217–225.
- Morris, W. et al. 2005. Environmental forcing and the competitive dynamics of a guild of cactus-tending ant mutualists. – *Ecology* 86: 3190–3199.
- Ness, J. H. et al. 2006. Variation in mutualistic potential among ant species tending extrafloral nectaries of *Ferocactus wislizeni*. – *Ecology*, in press.
- Oliveira, P. S. et al. 1999. Interactions between ants, extrafloral nectaries, and insect herbivores in Neotropical sand dunes: herbivore deterrence by visiting ants increases fruit set in *Opuntia stricta* (Cactaceae). – *Funct. Ecol.* 13: 623–631.
- Pickett, C. H. and Clark, W. D. 1979. The function of extrafloral nectaries in *Opuntia acanthocarpa* (Cactaceae). – *Am. J. Bot.* 66: 618–625.
- Price, M. V. et al. 2005. Temporal and spatial variation in pollination of a montane herb: a seven-year study. – *Ecology* 86: 2106–2116.
- Raine, N. E. et al. 2004. Guards and thieves: antagonistic interactions between two ant species coexisting on the same plant. – *Ecol. Entomol.* 29: 345–352.
- Rashbrook, V. K. et al. 1992. Anti-herbivore interactions: reasons for the absence of benefits to a fern with foliar nectaries. – *Ecology* 73: 2167–2174.
- Rhoades, D. 1979. Evolution of plant chemical defense against herbivores. – In: Rosenthal, G. A. and Janzen, D. H. (eds), *Herbivores: their interaction with secondary plant metabolites*. Academic Press, pp. 3–54.
- Rico-Gray, V. and Thien, K. B. 1989. Effect of different ant species on reproductive fitness on *Schomburgkia tibicinis* (Orchidaceae). – *Oecologia* (Berlin) 81: 487–489.
- Rudgers, J. A. and Gardener, M. C. 2004. Extrafloral nectar as a resource mediating multispecies interactions. – *Ecology* 85: 1495–1502.
- Rutter, M. T. and Rausher, M. D. 2004. Natural selection on extrafloral nectar production in *Chamaecrista fasciculata*: the costs and benefits of a mutualism trait. – *Evolution* 58: 2657–2668.
- Stanton, M. L. 2003. Interacting guilds: moving beyond the pairwise perspective on mutualisms. – *Am. Nat.* 162: S10–S23.
- Vasconcelos, H. L. and Davidson, D. W. 2000. Relationship between plant size and ant associates in two Amazonian ant-plants. – *Biotropica* 32: 100–111.
- Wäckers, F. L. and Bonifay, C. 2004. How to be sweet? Extrafloral nectar allocation by *Gossypium hirsutum* fits optimal defense theory predictions. – *Ecology* 85: 1512–1518.
- Warner, P. J. and Cushman, J. H. 2002. Influence of herbivores on a perennial plant: variation with life-history stage and herbivore species. – *Oecologia* 132: 77–85.
- Young, T. P. et al. 1997. Ants on swollen-thorn acacias: species coexistence in a simple system. – *Oecologia* 109: 98–107.
- Zangerl, A. R. and Rutledge, C. E. 1996. The probability of attack and patterns of constitutive and induced defense: a test of optimal defense theory. – *Am. Nat.* 147: 599–608.
- Zangerl, A. R. and Bazzaz, F. A. 1992. Theory and pattern in plant defense allocation. – In: Fritz, R. S. and Simms, E. L. (eds), *Plant resistance to herbivores and pathogens*. Univ. of Chicago Press, pp. 363–391.

Appendix 1. Simulations of cactus lifetime reproductive output.

The simulations focused on the direct impacts of ants on cactus reproductive success via reductions in attack by *Cabela ponderosella*, the pre-dispersal seed predator (Fig. 2b). For the sake of simplicity, I did not include in the simulations any indirect effects of ants on reproductive success via reductions in damage to vegetative parts (Fig. 2a). Therefore, the simulations generated conservative estimates of the positive effects of ants.

Parameters and equations that were common across all simulations are given in Table A1. The lifetime of a simulated plant involved the following five steps in each of 20 years (Fig. 1):

1. Early-season ant presence and identity

At the start of the growing season (May), a plant was identified as vacant or occupied by drawing a random variable from an age-dependent binomial distribution derived from a logistic regression of ant presence vs. age (Fig. 3a). If a plant was occupied, *Crematogaster* or *Liometopum* was assigned according to age-dependent probabilities.

2. Plant reproductive status and flower bud production

A plant was identified as either juvenile or reproductive by drawing a random variable from an age-dependent binomial distribution derived from a logistic regression of reproduction (yes/no) vs age (Table A1). For a reproductive plant, the number of flower buds it produced was linearly age-dependent. The slope of the relationship was drawn from a normal distribution with mean and standard deviation estimated from field data (Table A1). Cacti typically abort some proportion of the flower buds that they initiate, and this value was drawn from a beta distribution derived from field data (Table A1). Aborted flower buds made no contribution to seed production that year. However, I make the assumption that all flowers that do not abort successfully develop into fruits (i.e. no pollen limitation), which is supported by a previous study of the

pollination biology of *Opuntia imbricata* (McFarland et al. 1989).

3. Mid-season ant presence and identity

Later in the season (July), a plant was again identified as vacant or occupied, and occupied plants were assigned an ant species, by drawing random binomial variables as above (Step 1). The probabilities were dependent upon ant presence and identity early in the season.

4. Attack by pre-dispersal seed predators

For plants with fruits, the percentage of fruits that was attacked by *Cahela* larvae depended upon whether the plant was vacant, occupied by *Crematogaster*, or occupied by *Liometopum* at mid-season (step 3). Rates of *Cahela* attack were drawn from beta distributions with means and standard deviations specific to each ant occupancy state, estimated from the ant exclusion experiment (Fig. 2b, Table A1).

5. Seed production

The total number of seeds produced by a plant at the end of the season was equal to: the number of fruits without moth larvae times the number of seeds per fruit (drawn from a normal distribution; Table A1), plus the number of fruits with moth larvae times the number of seeds per fruit times the percent loss of seeds per fruit due to moth infestation (drawn from a beta distribution; Table A1).

Finally, I summed yearly seed production over the 20 years of plant growth to calculate lifetime reproductive output. Beta distributions are appropriate for simulating proportion data, as they are bounded by zero and one (Doak et al. 1994). I visually inspected histograms of all simulated data to ensure they showed a good fit to the field data. The simulations were programmed using Visual Basic in Microsoft Excel.

I constructed six versions of this simulation model that differed solely in the probabilities with which cacti interact with either species within and across years (steps 1 and 3). Table A2 shows, for each simulation, the equation used to estimate the probability that a plant was occupied at the start of the season (based on its age), and the conditional probabilities of either species occurring, given a plant was occupied. Table A3 shows, for each simulation, the conditional probabilities of mid-season ant occupancy and identity, given early-season status (based on rates of turnover given in Table 1).

References

- Doak, D. F. et al. 1994. Modeling population viability for the desert tortoise in the western Mojave desert. – *Ecol. Appl.* 4: 446–60.
- McFarland, J. D. et al. 1989. Pollination biology of *Opuntia imbricata* (Cactaceae) in southern Colorado. – *Can. J. Bot.* 67: 24–8.

Table A1. Parameter estimates and distributions common to all simulations of cactus lifetime reproductive success. Two parameters were age-dependent: probability of reproduction (logistic regression: $\chi^2 = 88.01$, $p < 0.0001$, $n = 120$) and flower bud production by reproductive plants (linear regression: $F = 127.85$, $p < 0.0001$, $R^2 = 0.67$, $n = 64$). Three parameters (number of seeds per fruit, percent reduction in seeds per fruit due to moths, and flower bud abortion rate) were independent of age. The number of seeds per fruit was estimated by dissecting fruits ($n = 67$) without moth larvae and counting seeds. The impact of moth larvae on seed production was estimated by comparing seed counts of infested fruits ($n = 13$) with expected seed numbers based on a linear regression of seed number vs. fruit mass ($F = 235.05$, $p < 0.0001$, $R^2 = 0.71$, $n = 94$). Moth attack rate was independent of age but depended upon the state of ant occupancy at mid-season (Fig. 2b). In each year of plant growth, parameter values were re-drawn from their respective distributions.

Parameter	Distribution	Equation or Mean (SD)
Probability of flowering	Binomial	$\frac{\exp(6.65 - 0.78 \times \text{age})}{1 + \exp(6.65 - 0.78 \times \text{age})}$
Number of flowerbuds	Normal	$0.91 (0.64) \times \text{age}$
Seeds per fruit	Normal	157 (96)
Percent reduction in seeds due to moth attack	Beta	0.55 (0.22)
Flowerbud abortion rate (% of initiated flowerbuds)	Beta	0.20 (0.28)
Moth attack rate (% of fruits with larvae)	Beta	<i>Liom.</i> : 0.05 (0.1) <i>Vacant</i> : 0.27 (0.27) <i>Crem.</i> : 0.19 (0.31)

Table A2. Probabilities of early-season ant status (presence and identity) used in simulations of cactus lifetime seed production. Table entries show the age-dependent probability of occupancy, which was consistent across all simulations (Fig. 3a), and the conditional probabilities of either species given a plant was occupied, which differed across simulations (see Fig. 3b for age-dependent probabilities used in simulations 1 and 4).

Simulation	Early-season probabilities		
	Pr(occupied)	Pr(<i>Crem.</i> occupied)	Pr(<i>Liom.</i> occupied)
1 <i>Liom.</i> > <i>Crem.</i> (observed)	$\frac{\exp(-1.9 + 0.26 \times \text{age})}{1 + \exp(-1.9 + 0.26 \times \text{age})}$	1-[Pr(<i>Liom.</i>)]	$\frac{\exp(-0.98 + 0.21 \times \text{age})}{1 + \exp(-0.98 + 0.21 \times \text{age})}$
2 <i>Liom.</i> only	$\frac{\exp(-1.9 + 0.26 \times \text{age})}{1 + \exp(-1.9 + 0.26 \times \text{age})}$	0.0	1.0
3 <i>Liom.</i> = <i>Crem.</i>	$\frac{\exp(-1.9 + 0.26 \times \text{age})}{1 + \exp(-1.9 + 0.26 \times \text{age})}$	0.5	0.5
4 <i>Crem.</i> > <i>Liom.</i>	$\frac{\exp(-1.9 + 0.26 \times \text{age})}{1 + \exp(-1.9 + 0.26 \times \text{age})}$	$\frac{\exp(-0.98 + 0.21 \times \text{age})}{1 + \exp(-0.98 + 0.21 \times \text{age})}$	1-[Pr(<i>Crem.</i>)]
5 <i>Crem.</i> only	$\frac{\exp(-1.9 + 0.26 \times \text{age})}{1 + \exp(-1.9 + 0.26 \times \text{age})}$	1.0	0.0
6 No ants	0.0	–	–

Table A3. Probabilities of mid-season ant status (presence and identity) used in simulations of cactus lifetime seed production under different scenarios of ant visitation. Mid-season occupancy was based on early-season ant status. Conditional probabilities of ant identity, given occupancy, were also dependent upon early-season ant status. Probabilities of occupancy for all simulations, and of species identity for simulations 1 and 4, were based on observed patterns of within-season turnover (Table 1).

Simulation	Early-season status	Mid-season probabilities		
		Pr(occupied early status)	Pr(<i>Crem.</i> occupied)	Pr(<i>Liom.</i> occupied)
1 <i>Liom.</i> > <i>Crem.</i> (Observed)	Vacant:	0.31	0.29	0.71
	<i>Crem.</i> :	0.67	0.79	0.21
	<i>Liom.</i> :	0.78	0.0	1.0
2 <i>Liom.</i> only	Vacant:	0.31	0.0	1.0
	<i>Liom.</i> :	0.78		
3 <i>Liom.</i> = <i>Crem.</i>	Vacant:	0.31	0.5	0.5
	Any ant:	0.72		
4 <i>Crem.</i> > <i>Liom.</i>	Vacant:	0.31	0.71	0.29
	<i>Crem.</i> :	0.78	1.0	0.0
	<i>Liom.</i> :	0.67	0.21	0.79
5 <i>Crem.</i> only	Vacant:	0.31	1.0	0.0
	<i>Crem.</i> :	0.67		
6 No ants	Vacant:	0.0	–	–