RICE UNIVERSITY

Context Dependent Species Interaction Outcomes in Ant-plant Protection Mutualisms

by

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

Master of Arts

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DECEMBER, 2008
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We often study the outcomes of species interactions, whether they be predation, competition, or mutualism, at one site in a single year. However, we increasingly recognize that species interaction outcomes are not static, but context dependent by varying along many ecological axes. Here, I asked to what extent and along what axes are ant-plant protection interactions, in which plants provide rewards for ants that in turn defend plants from herbivores, context dependent. First, a meta-analytic summary of published studies on ant-plant protection interactions revealed that interaction outcomes are on average mutualistic, and context dependency occurred due to plant reward type (domatia vs food bodies vs extrafloral nectaries), ant species richness, and latitude. Second, in a case study in the Sonoran Desert, extrafloral nectar production caused context dependent mutualistic and antagonistic ant-plant interactions, despite largely commensalistic interaction outcomes. These results suggest some ecological axes resulting in context dependency in mutualisms.
ACKNOWLEDGEMENTS

I would like to thank Juli Carrillo, David Guitierrez, Katherine Horn, Pamela Thompson, and Aline Waguespack for field and laboratory assistance in the Sonoran Desert; the National Park Service and Organ Pipe Cactus National Monument for logistical support; Juli Carrillo, Sarah Emery, Katherine Horn, Jennifer Rudgers, and Amy Savage, Ken Whitney, and anonymous reviewer's for their comments that improved earlier versions of these manuscripts; P. Ward assisted in the identification of ants. I am grateful to Nat Holland for his unwavering support and guidance through the duration of this thesis work. I am indebted to my committee members Evan Siemann and Jennifer Rudgers for their support throughout this thesis. Laura Johnson was very helpful in many regards. I was supported by a Wray Todd Fellowship throughout the duration of this master’s thesis. Of course, my loved ones Jeff and Janet Chamberlain ans sisters, and Katherine Horn made this all possible, by providing emotional support.
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CHAPTER 1: QUANTITATIVE SYNTHESIS OF CONTEXT DEPENDENCY IN ANT-PLANT PROTECTION MUTUALISMS

Note: Chapter 1 was submitted as a revised version on 8 August, 2008, with authors as Chamberlain and Holland. This manuscript is currently under revision in Ecology.
Abstract. Context dependency, variation in the outcome of species interactions with biotic and abiotic conditions, is increasingly considered ubiquitous among mutualisms. Despite several qualitative reviews of many individual empirical studies, there has been little quantitative synthesis examining the generality of context dependency, or conditions that may promote it. We conducted a meta-analysis of ant-plant protection mutualisms to examine the generality of context dependent effects of ants on both herbivory and plant performance (growth, reproduction). Our results show that ant effects on plants are not generally context dependent, but instead are routinely positive and rarely neutral, as overall effect sizes of ants in reducing herbivory and increasing plant performance were positive and significantly greater than zero. The magnitude of these positive effects did vary, however. Variation in plant performance was not explained by the type of biotic or abiotic factor examined, including plant rewards (extrafloral nectar, food bodies, domatia), ant species richness, plant growth form, or latitude. With the exception of plant growth form, these factors did contribute to the effects of ants in reducing herbivory. Reductions in herbivory were greater for plants with than without domatia, and greatest for plants with both domatia and food bodies. Effect sizes of ants in reducing herbivory decreased, but remained positive, with both latitude and ant species richness. Although studies of ant-plant interactions have been pivotal in the study of context dependency of mutualisms, our results, along with other recent meta-analyses, indicate that context dependency may not be a general feature of mutualistic interactions. Rather, ant-plant protection mutualisms appear to be routinely positive for plants, and only occasionally neutral.
Key words: ant-plant interaction; conditionality; context dependency; domatia; extrafloral nectar; food body; herbivory; interaction strength; meta-analysis; protection.
INTRODUCTION

Although species interactions are often described by their outcomes, including predation (+,-), competition (-,-), mutualism (+,+), and commensalism (+,0), they are not static, but vary along a continuum in which outcomes grade into one another. The causes and consequences of context dependency, or variation in interaction outcomes with biotic and abiotic factors, has attracted increasing attention (Bronstein 1994, Agrawal et al. 2007). Understanding whether interactions are in general context dependent, and what factors contribute to context dependency, will help aid in our understanding of species interactions. Attention to context dependency is particularly widespread in the study of mutualistic interactions, which are now commonly thought to readily grade into commensalism or parasitism under a variety of conditions. In keeping with empirical studies and qualitative reviews highlighting its importance (Bronstein 1994, Herre et al. 1999, Hay et al. 2004, Holland et al. 2005, Stadler and Dixon 2005, Bronstein et al. 2006, Sachs and Simms 2006, Heath and Tiffin 2007, Rico-Gray and Oliveira 2007, Romero et al. 2008), context dependency has even been touted as one of the few generalizations that can be made of mutualism (Bronstein 1994, Holland and Bronstein 2008). Despite such consensus, the generality of context dependency of mutualism has not been examined quantitatively. In fact, a recent meta-analysis of plant-mycorrhizal mutualisms revealed routinely positive, rather than context dependent effects of ectomycorrhizae on plant biomass and growth (Karst et al. 2008).

In addition to plant-mycorrhizal interactions, ant-plant protection mutualisms have also contributed to the perception that context dependency is generally common in mutualistic interactions (Bronstein 1994, 1998). The effects of ants in reducing herbivory
and increasing plant performance (growth, reproduction) may not always be positive
(mutualism), but may include neutral (commensalism) or negative (parasitism) effects.
Given that ant-plant protection interactions involve a third party (plant herbivores),
interaction outcomes between ants and plants may be more prone to context dependency
than other mutualisms not involving a third party (e.g., pollination). Indeed, ant-plant
protection interactions are not universally mutualistic, and may depend on local biotic
and abiotic conditions in which interactions occur (e.g., Gastreich 1999, Kersch and
Fonseca 2005). For example, ant species identity and abundance were both important in
determining variable plant benefits from ant protection in desert (Gossypium hirsutum)
and tropical (Dioscorea praehensilis) plant species (Di Giusto et al. 2001, Rudgers and
Strauss 2004). Several qualitative reviews have recently synthesized studies of ant-plant
protection interactions, highlighting key progress in our understanding of them and their
contributions to our knowledge of mutualism, including context dependency (Beattie
1985, Davidson and Epstein 1989, Huxley and Cutler 1991, Davidson and McKey 1993,
and Oliveira 2007). Nonetheless, we currently have no quantitative synthesis of the
generality of context dependency for ant-plant protection interactions or the biotic and
abiotic factors contributing to it.

In this study, we examined the extent of context dependency in ant-plant
protection mutualisms using meta-analysis, a technique that incorporates variation in the
precision and statistical power of individual studies (Gurevitch and Hedges 1999, Gates
2002). If ant effects on herbivory and plant performance are routinely context dependent,
then mean effect sizes (ratio of plant response with ants : without ants) are predicted not
to deviate from zero. Alternatively, if ant-plant interactions are regularly mutualistic, rather than context dependent, then mean effect sizes of ants in reducing herbivory and increasing plant performance are predicted to be positive and greater than zero. In addition to testing these predications for overall ant effects on plants, we also examined if these predictions for the effect sizes of ants on plants varied with several biotic and abiotic conditions. First, the effects of ants on plants may vary with the rewards supplied by plants (domatia, extrafloral nectar, and food bodies), which mediate their consumer-resource interactions with ants (Holland et al. 2005). Moreover, obligate interactions are often associated with domatia-bearing plants that house ant colonies (myrmecophytes), whereas non-domatia bearing plants do not house interacting ants (myrmecophiles; Davidson and McKey 1993). Second, because plants that interact with ants range from herbaceous annuals to long-lived trees, the benefits of ants may vary with plant growth form (Bronstein 1994). Third, the number of ant species interacting with a plant may influence effect sizes of ants, possibly through interspecific competition among ants (Stanton 2003, Miller 2007). Fourth, variation in the effects of ants on plants may occur with latitude, given that ant-plant interactions span tropical, sub-tropical, desert, and temperate ecosystems. Lastly, we examined if herbivory and plant performance benefits varied with methodological practice, and if our results were contingent upon the file drawer effect for insignificant results. While a number of other important biotic and abiotic factors may be important to the context dependency of ant-plant interactions, we examined the above factors as they were most commonly reported among published studies (Appendix A).
METHODS

We surveyed the primary literature using Web of Science and citations within reviews of ant-plant protection interaction studies (Davidson and McKey 1993, Bronstein 1998, Heil and McKey 2003, Bronstein et al. 2006). We included studies that performed ant exclusion experiments (ants removed or prevented from accessing plants) and those that used the natural presence and absence of ants on plants. We assigned each study to one or both of two plant responses: herbivore damage and herbivore density (hereafter, herbivory), and plant growth and reproduction (hereafter, plant performance). For both herbivory and plant performance, we used mean values for records that were not independent (e.g., different years, populations, study sites, or multiple measures of the same response variable). We included each plant species when more than one was reported within a single paper. We combined records among studies of the same plant species. Importantly, we only incorporated studies into our data set that reported error estimates along with mean values. The data set includes 76 studies, representing 64 plant species in 28 families (Appendix A).

We quantified the effect size of ants on herbivory and plant performance using the response ratio, as it assumes that effects are multiplicative, which is likely more biologically appropriate than assuming additive effects (e.g., Hedges' $d$) (Sih et al. 1998). We performed statistical analyses, and graphically depicted results, using the $ln$ transformed response ratio, $L$, as it is less sensitive to errors in the effect size ratio denominator (Hedges et al. 1999). Although the response ratio is usually calculated as $L = \frac{X_E}{X_C}$, where $X_E$ and $X_C$ are means of experimental (ant exclusion) and control (ant access) groups, respectively, $L$ was inverted and calculated as $ln\left(\frac{X_C}{X_E}\right)$. In this way,
the sign of the effect size reflects negative or positive effects of ants on plants. For herbivory, we reversed the sign of the effect of ants on herbivory prior to calculating the effect size to express the effect size in a consistent manner with that of ants on plant performance. Thus, when \( L = 0 \), ants had no effect on herbivory or plant performance; when \( L > 0 \), ants had a positive effect on plants by reducing herbivory or increasing plant performance; and, when \( L < 0 \), ants had a negative effect on plants by increasing herbivory or reducing plant performance.

For each set of analyses described below, we estimated mean effect sizes (\( \bar{L} \)) and their 95% confidence intervals using resampling tests with 999 iterations (Rosenberg et al. 2000). We used a random effects model that assumed the true effect size may vary among studies, which is a reasonable assumption given the variety of methods employed among the data sets included (Gurevitch and Hedges 2001). Confidence intervals that not bracketing zero differed significantly from zero (\( \alpha = 0.05 \)). We report weighted mean effect sizes (\( \bar{L} \)) among studies and confidence intervals as \( \bar{L} = \frac{\sum_{i=1}^{n} w_i E_i}{\sum_{i=1}^{n} w_i} \) and

\[
L \pm t_{\alpha/2(n-1)} \times S_L,
\]

where \( w_i = 1/S_i^2 \) and \( E_i \) is the effect size for the \( i \)th study. \( S_L \) is the standard deviation of \( L \), \( S_L = \sqrt{\left(\frac{S_E^2}{N_E} + \frac{S_C^2}{N_C} \right) + \left(\frac{S_E^2}{N_E} + \frac{S_C^2}{N_C} \right)} \), where \( S_E \) and \( S_C \) and \( N_E \) and \( N_C \) are the standard deviations and sample sizes of experimental and control groups, respectively. When multiple measures of herbivory or plant performance were not independent for the same plant species within the same or different papers, we computed a mean \( L \) for those measures, as well as a mean standard deviation

\[
\bar{S}_L = \sqrt{\frac{\sum_{i=1}^{n} S_i^2 N_i}{\sum_{i=1}^{n} N_i - n}},
\]

where \( N_i \) is the sample size for the \( i \)th study. For all analyses described below, we used homogeneity statistics in MetaWin Version 2.2 (Rosenberg et
al. 2000). For categorical models, the among-group sum of squares ($Q_B$) was compared to the critical value ($\alpha = 0.05$) of the chi-square distribution ($df = n - 1$). For continuous models, we used weighted least squares regression, in which variation in effect sizes explained by the independent variable ($Q_{reg}$) was compared to the critical value ($\alpha = 0.05$) of the chi-square distribution ($df = 1$). $Q_B$ and $Q_{reg}$ were calculated as described by Rosenberg et al. (2000).

Using the above-described protocols, we conducted a series of analyses to examine the effects of ants on herbivory and plant performance, and the contribution of multiple factors to such effects. First, we tested whether overall ant effects on herbivory and plant performance differed from zero, and whether the effect size of ants on herbivory differed from that on plant performance. Second, we tested whether effect sizes of reduced herbivory correlated with effect sizes of increased plant performance by calculating a $P$-value based on comparing the observed Pearson correlation coefficient $r$ (null hypothesis $r = 0$) to the distribution of $r$'s from Monte Carlo randomizations (9999 iterations) of the data set. The data set for this analysis included studies with and without error estimates (Appendix A) to obtain a larger sample size for this analysis. In this analysis species are replicates, and a mean value was used for each species. Note that patterns from a within species analysis may be quite different from our among-species analysis here, but the data are not available to conduct a within species analysis.

Third, we conducted a series of analyses to examine the contributions of multiple biotic and abiotic factors to the effect sizes of ants on herbivory and plant performance. We examined whether effect sizes for herbivory and plant performance differed between plants with (myrmecophytes; Mt) and without (myrmecophiles; Ml) domatia. We also
evaluated whether effect sizes of ants on plants varied with the type of plant reward supplied to ants. For this study, we refer to food, pearl, beltian, and mullerian bodies collectively as food bodies (F); to various types of nectaries outside of flowers as extrafloral nectaries (E); to shelter or housing provided by plants as domatia (D). We also include an 'other' category (O) for trophobionts such as aphids which may attract ants to plants and aid in plant protection (Messina 1981). In total, we examined differences in effect sizes among six types or combinations of plant rewards (food bodies, extrafloral nectar, and domatia). Given different biologies of plants associated with their growth forms (Harper 1977), we examined the extent to which effect sizes varied with plant growth form (shrub [Sh], annual herb [Ah], succulent [Su], tree [Tr], liana [Li], and perennial herb [Ph]). We tested for differences in effect sizes among these plant groups using a random effects model and $Q_b$, as described above. Alternatively, benefits of ant protection for herbivory and plant performance may vary with the number of ant species interacting with plants. We examined whether effect sizes for herbivory and plant performance varied with ant species richness using random effects regression analyses as described above. Lastly, we examined whether effect sizes of ants on herbivory and plant performance varied with latitude, a reasonable proxy for large-scale variation in the abiotic environment. We used random-effects regression analysis with herbivory and plant performance as response variables and the absolute value of latitude (to 0.1 degrees) of each study as the explanatory variable.

Fourth, we explored the influence of methodological variables on the effect sizes of ants on herbivory and plant performance. Specifically, we tested whether experimental (EX; ant exclusion, control) and non-experimental (NE; natural presence/absence of ants)
methods influenced effect sizes using a random effects model and $Q_B$ as described above. Studies also varied in the use of plants (Pl), branches (Br), leaves (Lv), or reproductive parts (Rep) as the unit of replication. We tested whether these units of replication influenced effect sizes using a random effects model and $Q_B$ as described above. The duration over which individual studies occurred varied from one to three years. We performed a random-effects regression analysis, for both herbivory and plant performance, with effect sizes as a function of study duration, and calculated $Q_{reg}$ as described above. Lastly, we investigated publication bias in the reporting of ant-plant protection studies using Rosenthal’s method ($\alpha = 0.05$) to calculate fail-safe values for each of herbivory and plant performance.

**RESULTS**

The overall effect size of ants on plants was positive and significantly different from zero for both herbivory ($\bar{L}$ [95% CI], 0.93 [0.67-1.21]; Fig. 1.1a) and plant performance (0.25 [0.06-0.46]; Fig. 1.1b), though the mean effect size for herbivory was significantly greater than that of plant performance ($Q_B = 18.4$, df = 1, $P < 0.0001$). These overall effect sizes indicate that ants do generally reduce herbivory and increase plant performance, and thus ants are on average beneficial for plants. Over all possible influences that we examined, no single factor resulted in a significantly negative mean effect size, and most 95% CI’s of positive effect sizes did not include zero. These results indicate that among species context dependent outcomes are not common in ant-plant protection interactions. Nevertheless, 5 of 24 variables in Fig. 1.1 did have effect sizes that were not significantly positive (i.e., confidence intervals overlapped zero),
suggesting some context dependent commensalism. These five cases were limited to
effect sizes for plant performance, for which sample sizes also tended to be small, which
could reduce statistical power.

For those studies reporting both herbivory and plant performance, the positive
effects of ants on herbivory were not positively correlated with the positive effects of ants
on plant performance ($P = 0.09, n = 14$; Fig. 1.2). This insignificant result was unchanged
by removing the outlier (top right data point, Fig. 1.2, $P = 0.245, n = 13$). Thus, ant
effects on plant herbivory did not necessarily translate into proportional changes in plant
performance, suggesting that, within a plant species, it is best to measure both responses
to accurately capture the effects of ants.

Four factors contributed to effect sizes of ants on herbivory and plant
performance. First, the effect size of ants in reducing herbivory was greater for plants
with domatia (myrmecophytes, Mt) than without domatia (myrmecophiles, Ml) ($Q_B =
7.99, df = 1, P = 0.005$; Fig. 1.1a). No difference for plant performance effect sizes
occurred between myrmecophytes and myrmecophiles ($Q_B = 1.13, df = 1, P = 0.287$; Fig.
1.1b), though only five records occurred for myrmecophytes. Second, plant rewards
(domatia, food bodies, extrafloral nectar) provided to ants affected variation in the
magnitude of the positive effect sizes of ants in reducing herbivory ($Q_B = 14.7, df = 5, P
= 0.012$; Fig. 1.1a), but did not contribute to plant performance ($Q_B = 1.01, df = 2, P =
0.602$; Fig. 1.1b). In particular, the greatest effect size of ants in reducing herbivory
occurred for plants that provisioned both domatia and food bodies, whereas those
providing only extrafloral nectar tended to have the smallest, yet positive effect size (Fig.
1.1a). The only plant reward not to provide a significant positive effect on plants was the
'other' category (O) for plant performance. Plant growth form did not contribute to the magnitude of the positive effect sizes of ants on reducing herbivory \( (Q_B = 1.00, \text{df} = 2, P = 0.608; \text{Fig. 1.1a}) \) or increasing plant performance \( (Q_B = 5.77, \text{df} = 5, P = 0.329; \text{Fig. 1.1b}) \). However, unlike effect sizes for herbivory, effect sizes on plant performance did not always differ from zero, including in particular those of annual herbaceous plants (Ah), trees (Tr), and lianas (Li). Third, effect sizes of ants in reducing herbivory decreased, but remained positive, with increasing species richness of ants interacting with plants \( (Q_{\text{reg}} = 4.86, \text{df} = 1, P = 0.027; \text{Fig. 1.3a}) \). No such relationship was observed for plant performance \( (Q_{\text{reg}} = 0.02, \text{df} = 1, P = 0.891; \text{Fig. 1.3b}) \). Fourth, effect sizes of ants in reducing herbivory decreased, but remained positive with increasing latitude \( (Q_{\text{reg}} = 9.42, \text{df} = 1, P = 0.003; \text{Fig. 1.4a}) \), but showed no relationship with plant performance \( (Q_{\text{reg}} = 1.01, \text{df} = 1, P = 0.316; \text{Fig. 1.4b}) \).

In addition to biotic and abiotic conditions, methodological biases may contribute to the effect sizes of ants in reducing herbivory and increasing plant performance. Effect sizes varied with the type of unit of replication (reproductive parts, leaves, branches, or plants) for herbivory \( (Q_B = 90.3, \text{df} = 2, P < 0.0001; \text{Fig. 1.5a}) \) and plant performance \( (Q_B = 16.5, \text{df} = 2, P < 0.0001; \text{Fig. 1.5b}) \); however, sample sizes for reproductive parts, leaves, and branches were small \( (n = 2-5) \). Studies that excluded ants experimentally had smaller mean effect sizes than those relying on natural presence and absence of ants, for both herbivory \( (Q_B = 3.94, \text{df} = 1, P = 0.047; \text{Fig. 1.5a}) \) and plant performance \( (Q_B = 5.64, \text{df} = 1, P = 0.018; \text{Fig. 1.5b}) \). However, although sample sizes varied, non-experimental studies showed greater variation around the mean effect size than did experimental studies for both herbivory (% increase in CI width from experimental to
non-experimental studies: 620%) and plant performance (105%). Studies varied in
duration, ranging from 1-3 years, with 80% of studies occurring in one year only.
Nevertheless, effect sizes did not vary with study duration for herbivory ($Q_{reg} = 0.08$, df =
1, $P = 0.779$) or plant performance ($Q_{reg} = 0.54$, df = 1, $P = 0.464$).

    Last, the lack of context dependency and overwhelmingly positive effects of ants
in reducing herbivory and increasing plant performance may simply arise from a
publication bias towards those studies with positive results. We used Rosenthal's method
to calculate the number of non-significant studies necessary to change these results from
significant to insignificant. The fail-safe value for the number of studies was 924 for
herbivory and 109 for plant performance, suggesting that results are robust to the file-
drawer effect for studies with insignificant results. Funnel plots (not shown here) also
showed little bias in the data set.

DISCUSSION

    We performed a meta-analysis to examine quantitatively the common perception
that ant-plant protection mutualisms are typically context dependent, that is, their
interaction outcomes routinely vary from mutualism to commensalism or parasitism
depending on biotic and abiotic conditions. Our results demonstrate that, rather than
context dependent interactions, ants do generally interact mutualistically with plants by
reducing herbivory and increasing plant performance (reproduction, growth).
Nevertheless, we did identify some factors that affect the magnitude of the positive effect
sizes of ants on plants, particularly for herbivory response variables. We discuss
implications of these results for the context dependency of mutualistic interactions in
general, along with some potential directions for future research.

This finding that ant-plant protection mutualisms are not generally context
dependent is consistent with the few other quantitative analyses of mutualistic
interactions. A recent meta-analysis of plant-mycorrhizal interactions showed that effect
sizes of ectomycorrhizae on plant biomass and growth were generally positive and did
not depend contextually on partner identity or abundance, duration of association, or
phosphorus levels (Karst et al. 2008). In another recent meta-analysis, effect sizes of
pollinators, ecto- and arbuscular mycorrhizae, and bacteria on plant performance were all
significantly positive (Morris et al. 2007). It appears then that effects of a variety of
mutualists on another are not generally context dependent, as neutral and negative effects
were not sufficiently frequent to shift mean effect sizes from significantly positive to
neutral or negative. While ant-plant protection interactions can certainly be context
dependent in individual cases given local biotic and abiotic conditions within a species
(e.g., Gastreich 1999, Kersch and Fonseca 2005, Chamberlain and Holland 2008), it
appears that context dependent shifts of mutualism to commensalism or parasitism are
not the rule, but rather an exception.

We identified several factors that explained variation in the magnitude of the
generally positive effects of ants on plants. First, as ant-plant protection mutualisms are
mediated by the rewards (domatia, food bodies, extrafloral nectar) supplied by plants, it is
not surprising that the type of plant reward influenced the magnitude of effects on
herbivory. The most prominent difference was due to domatia; plants providing housing
for ants had a substantially larger reduction in herbivory than plants without such
structures. This result is consistent with phytoecious ants that live on myrmecophytic plants being particularly aggressive in defense of host plants (Heil and McKey 2003). Plant species supplying both domatia and food bodies [e.g., *Cecropia, Macaranga, Maieta, Piper*; (Schupp 1986, Fiala et al. 1989, Vasconcelos 1991, Letourneau 1998)] showed the greatest reduction in herbivory among the various types and combinations of rewards supplied by plants. Plants producing extrafloral nectaries and an additional reward such as food bodies or domatia experienced significantly greater reductions in herbivory than those producing extrafloral nectaries alone. Plant rewards, that is a cost of mutualism (Bronstein 2001), contributed to variation in the magnitude of ant effects on plants. In this regard, further attention may need to be given to the role of such costs in understanding mutualistic interactions and the magnitude of their interaction strengths.

In addition to rewards supplied by plants, both latitude and ant species richness contributed to the magnitude of the positive effects of ants on herbivory. Benefits via reduced herbivory declined from the equator to the poles, consistent with the hypothesis that higher precipitation and temperatures correspond with greater benefits. However, the fraction of plants with domatia (myrmecophytes) or extrafloral nectaries also decreases from the equator to the poles (Heil and McKey 2003, Rico-Gray and Oliveira 2007), making it difficult to separate abiotic and biotic mechanisms. In addition, interacting with fewer ant species was associated with greater reductions in herbivory. This pattern could result if more ant species per plant increases the probability that an ant species cheats (removes reward without conferring benefit), or if more ant species increases competition among ants for plant rewards, thereby decreasing plant protection. The decrease in benefit with both increasing latitude and ant species richness may appear contradictory,
given that ant species richness generally declines with latitude in other studies (Cushman et al. 1993). However, in our data set, ant richness on plants increased at higher latitudes (n = 56 plant species, \( \rho = 0.48, P = 0.0002 \)), and obligate ant-plant interactions (which tend to include only one or a few ant species) declined at higher latitudes (Heil and McKey 2003). Latitude and ant species richness are proximate variables for some other underlying factor that contributes to the magnitude of positive effects sizes of ants on plants. Whether effects are ultimately attributable to abiotic or biotic factors, there is a trend for greater reductions in herbivory both at lower latitudes and lower ant species richness.

Although these biotic and abiotic variables influence ant effects on plants, methods used to study ant-plant protection interactions also influence our conclusions about context dependency. Overall, the effect size of ants in reducing herbivory was 270% larger than for increased plant performance; this may reflect a real pattern, but is also likely influenced by fewer studies that measure plant performance (Fig. 1.1). Our results point to the need for more studies that quantify both herbivory and plant performance, as we identified only 14 species for which both responses were measured in the same study. Instead of methodological reasons, the lack of association between herbivory and plant performance may arise from biological factors, most notably that other direct and indirect interactions plants have with mutualists (e.g., pollinators) and antagonists (e.g., herbivores) may curtail individual effects of particular pairwise ant-plant interactions (Morris et al. 2007). The generality of conclusions from ant-plant protection studies will greatly benefit from more direct measures of plant fitness, including reproduction, growth, and per-capita growth rates. The unit of replication and
whether studies experimentally excluded ants also contributed to variation in effect sizes. Leaves and branches overestimated and reproductive parts underestimated (relative to whole plants) positive ant effects on plants, respectively. We suggest that future studies avoid fractional treatment application below the whole plant level. Furthermore, studies that used natural presence and absence of ants inflated the positive effects of ants on plants relative to studies that experimentally excluded ants. Remedying these methodological issues will lead to a greater understanding of ant-plant protection mutualisms.

We have shown that ant effects on plants are consistently positive, and rarely neutral, suggesting that mutualisms may not be as context dependent as previously thought (Bronstein 1994, Holland and Bronstein 2008). Although context dependency does not appear common among species in ant-plant protection or plant-mycorrhizal interactions (Karst et al. 2008), it may be relatively more important among individuals or populations within a species. Past ant-plant protection studies have sought to understand if ant-plant interactions are on average mutualistic (Bronstein 1998). However, a greater understanding of the extent of context dependency in ant-plant protection interactions and mutualism in general, and the factors that contribute to it, will emerge from future studies explicitly studying interaction outcomes along gradients of abiotic (e.g., precipitation, nutrients) and biotic (e.g., partner identity, abundance, rewards) factors.

Acknowledgements

We thank J. Carrillo, K. Horn, J. Rudgers, and A. Savage, and anonymous reviewer’s for their comments that have improved earlier versions of this manuscript.
References


Fig. 1.1 Mean effect sizes [response ratios, $\ln(\bar{X}_c/\bar{X}_e)$] and 95% confidence intervals (CI) of ants on herbivory (a) and plant performance (b). When a 95% CI does not overlap zero, the effect size is significantly different from zero. Dotted lines show effect sizes of zero. Mean effect sizes $> 0$ represent a reduction in herbivory or an increase in plant performance, whereas mean effect sizes $< 0$ represent an increase in herbivory or a reduction in plant performance. Effect sizes are reported for four separate analyses: (1) 'Overall' ant effects combines all studies; (2) 'Domatia' compares plants with (myrmecophytes; Mt) and without domatia (myrmecophiles; Ml); (3) 'Plant reward' examines the plant rewards provided to ants, including domatia (D), extrafloral nectar (E), food bodies (F), domatia and food bodies (DF), extrafloral nectar and food bodies (EF), domatia and extrafloral nectar (DE), and other (O, hemipteran excretions); and (4), 'Plant growth form' of shrub (Sh), annual herb (Ah), succulent (Su), tree (Tr), liana (Li), and perennial herb (Ph). Sample sizes are reported in the top of each panel. ** denotes significance ($P < 0.05$) of the $Q_B$-values of the four analyses.
Fig. 1.2 Plot of effect sizes [response ratios, \( \ln(\bar{X}_c/\bar{X}_e) \)] of herbivory versus plant performance for studies in which both variables were measured. Dotted lines show effect sizes of zero.
Fig. 1.3 Effect sizes [response ratios, $ln(\bar{X}_c / \bar{X}_E)$] of ants on herbivory (a) and plant performance (b) as versus ant species richness. Dotted lines show effect sizes of zero. Linear regression lines are shown for significant relationships with $Q_{reg}$ compared to the critical value ($\alpha = 0.05$) of the chi-square distribution (df = 1).
Fig. 1.4 Effect sizes [response ratios, \( \ln(\bar{X}_c / \bar{X}_e) \)] of ants on herbivory (a) and plant performance (b) as versus latitude. Dotted lines show effect sizes of zero. Linear regression lines are shown for significant relationships with \( Q_{reg} \) is compared to the critical value (\( \alpha = 0.05 \)) of the chi-square distribution (df = 1).
Fig. 1.5. Analyses of methodological influences on effect sizes [response ratios, \( \ln(\bar{X}_C / \bar{X}_E) \)] of ants on herbivory (a) and plant performance (b) with sample sizes reported in the top of each panel. Dotted lines show effect sizes of zero. When a 95% CI does not overlap with zero, the effect size is significantly different from zero. Mean effect sizes > 0 represent a reduction in herbivory or an increase in plant performance, whereas mean effect sizes < 0 represent an increase in herbivory or a reduction in plant performance. Mean effect sizes are reported for two separate analyses: (1) the unit of replication of the study being reproductive parts (flower, fruits; Rep), leaves (Lv), branches (Br) or plants (Pl), and (2) natural presence and absence of ants (NE) versus experimental manipulation (EX) of ant presence and absence. Significance of associated \( Q_b \)-values are *** \( P < 0.001 \) and ** \( P < 0.05 \).
Appendix 1.A. List of records used in the meta-analysis, followed by full citations. Table includes literature source, plant species and family, study duration (yrs), whether the study experimentally excluded ants or used natural presence/absence of ants (E: yes [y]/no [n]), plant growth form (Pgf), plant reward that mediates the ant-plant interaction studied (Pr), unit of replication for the experiment or study (Rp), whether the study provided error estimates or not (V: yes [y]/no [n]), and the In response ratio (L). Study duration (Sd, years) combines years for plant species in which multiple studies were averaged. Plant rewards used by ants include domatia (D), extrafloral nectaries (E), food bodies (F), other (e.g., homopteran exudates), and their combinations (e.g., DE). Responses of plants measured in the original study and used in the meta-analyses herein include plant performance (PP) and herbivory (H). The log$_e$ response ratio, $L$, (log$_e$ ($\frac{X_C}{X_E}$)) was calculated for each record as described in Methods.

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Full citations of studies listed in Appendix 1.A.


CHAPTER 2: DENSITY-MEDIATED AND CONTEXT-DEPENDENT CONSUMER-RESOURCE INTERACTIONS BETWEEN ANTS AND EXTRAFLORAL NECTAR PLANTS

Note: Chapter 2 was accepted for publication in Ecology as an Article on 11 September, 2007, with authors as Chamberlain and Holland.
Abstract. Interspecific interactions are often mediated by the interplay between resource supply and consumer density. The supply of and a consumer's density response to one resource may in turn yield context dependent use of other resources. Such consumer-resource interactions occur not only for predator-prey and competitive interactions, but mutualistic ones as well. For example, consumer-resource interactions between ants and extrafloral nectar (EFN) plants are often mutualistic, as EFN resources attract and reward ants that protect plants from herbivory. Yet, ants also commonly exploit floral resources, leading to antagonistic consumer-resource interactions by disrupting pollination and plant reproduction. EFN resources associated with mutualistic ant-plant interactions may also mediate antagonistic ant-flower interactions through the aggregative density response of ants on plants, which could either exacerbate ant-flower interactions or alternatively satiate and distract ants from floral resources. In this study, we examined how EFN resources mediate the density response of ants on senita cacti in the Sonoran Desert, and their context dependent use of floral resources. Removal of EFN resources reduced the aggregative density of ants on plants, both on hourly and daily time scales. Yet, the increased aggregative ant density on plants with EFN resources decreased rather than increased ant use of floral resources, including contacts with and time spent in flowers. Behavioral assays showed no confounding effect of floral deterrents on ant-flower interactions. Thus, ant use of floral resources depends on the supply of EFN resources, which mediates the potential for both mutualistic and antagonistic interactions by increasing the aggregative density of ants protecting plants, while concurrently distracting ants from floral resources. Nevertheless, only certain years and populations of study showed an increase in plant reproduction through herbivore protection or ant
distraction from floral resources. Despite pronounced effects of EFN resources mediating
the aggregative density of ants on plants and their context dependent use of floral
resources, consumer-resource interactions remained largely commensalistic.

Key words: antagonism; ant-plant interaction; commensalism; consumer-
resource interaction; context-dependent; density-mediated; distraction; extrafloral
nectar; flower; mutualism; protection; senita.
INTRODUCTION

Central to the study of interspecific interactions is understanding the interplay between the availability and supply of resources and consumer density. The supply of resources, whether prey of predators or limiting resources of competitors, is essential to a consumer's density response to interspecific interactions, and resulting dynamics of the interacting species (Tilman 1982, Murdoch et al. 2003, Turchin 2003). Density responses of consumers to the supply of resources may manifest as functional or numerical responses, or as an aggregative density response, that is a short-term behavioral change in the number of consumers aggregating with the supply of resources (Turchin 2003). The supply of and a consumer's density response to one resource may in turn yield context dependent use of and effects on another resource, such as that exemplified by apparent competition (Holt 1977, Abrams et al. 1998). Such consumer-resource interactions are well recognized to form the basis of both predation and competition (Murdoch et al. 2003, Turchin 2003), but little consideration has been given to mutualism as a consumer-resource interaction. Yet, nearly all mutualisms are consumer-resource interactions, one species functioning as a consumer and the other as a resource (Holland et al. 2005). Mutualists produce resources that mediate their interactions by attracting and rewarding the consumers with which they interact. For example, plants produce nectar and fruit resources that attract and reward pollinators and seed dispersers; mycorrhizal fungi and rhizobial bacteria obtain carbohydrate resources from plants and supply nutrients to them; and, food excretions by hemipterans and sugar secretions by lycaenid caterpillars attract and reward ants in exchange for protection from natural enemies. Because mutualism, like predation and competition, is a consumer-resource interaction, it too may depend
critically on the interplay between the supply of resources and density responses of consumers, both of which may be key factors contributing to the well-established context dependency of their interactions (Bronstein 1994, Agrawal et al. 2007).

Consumer-resource interactions between ants and plants abound in nature, ranging from mutualistic protection to antagonistic florivory, herbivory, and granivory (Hölldobler and Wilson 1990). Mutualistic ant-plant interactions are mediated by a wide variety of resources produced by plants, such as beltian bodies, domatia, eliasomes, and extrafloral nectar. Of particular ubiquity in nature are ant-plant interactions mediated by extrafloral nectar (EFN) resources (nectar not associated with pollination), with species of >25% of angiosperm families, including 332 genera, bearing EFN resources (Koptur 1992). Consumer-resource interactions between ants and EFN plants are often mutualistic, as EFN resources attract and reward ants that protect plants from herbivory (Bronstein 1998, Heil and McKey 2003, Bronstein et al. 2006). However, ants also commonly exploit floral resources, which results in antagonistic interactions by disrupting pollination and plant reproduction through florivory, pollen consumption, pollinator interference, reduced pollen viability, and depletion of floral nectar (Galen 1983, Beattie et al. 1984, Rico-Gray 1993, Visser et al. 1996, Puterbaugh 1998, Galen 2005, Junker et al. 2006, Ness 2006).

Although commonly associated with mutualistic interactions, EFN resources may also mediate antagonistic ant-flower interactions through the behavioral, aggregative density response of ants on plants. If the aggregative density response of ants on plants increases with EFN resources, then ant-flower interactions may also increase simply due to their greater abundance on plants. Alternatively, the supply of EFN resources may
distract and satiate ants, thereby reducing their use of floral resources (Wagner and Kay 2002). Yet, flowers may have properties that deter and repel ants from using them as resources (Ghazoul 2001, Junker et al. 2006, Ness 2006). Thus, ant use of floral resources may depend contextually on the supply of EFN resources, the aggregative density responses of ants, and whether flowers repel ants. If floral deterrents do not occur, then both mutualistic ant-plant interactions and antagonistic ant-flower interactions may depend on the interplay between the supply of EFN resources and aggregative density responses of ants on plants. Even though plant protection and ant distraction resulting from the supply of EFN resources are not mutually exclusive, both feasibly operating in concert with one another, little attention has been given to whether antagonistic ant-flower interactions depend contextually on the supply and availability of EFN resources.

Using a guild of ants interacting with EFN-bearing senita cacti in the Sonoran Desert, we studied how the supply of EFN resources mediates the behavioral, aggregative density response of ants on plants and their context dependent use of floral resources. Specifically, we addressed the following questions: Do floral chemicals deter ants from utilizing floral resources? Does the behavioral, aggregative density response of ants on plants vary with the availability of EFN resources? Do ant-flower interactions increase with the supply of EFN resources, or alternatively do EFN resources distract ants from interacting with floral resources? Do ants increase plant reproduction through herbivore protection and/or reduce plant reproduction by interacting with flowers and disrupting pollination processes?

METHODS
Study system — We studied interactions between senita cacti (*Pachycereus schottii* Engelmann) and a guild of ants at Organ Pipe Cactus National Monument (OPCNM) in Arizona during the spring and summer flowering season of 2006. Senita is a multi-stemmed columnar cactus attaining heights of 2-4 m and can live for >75 years. Senita produce 10-40 flowers per night from April through July at OPCNM. Hermaphroditic flowers have an inferior ovary containing many ovules, 100s of anthers, one pistil, and a lobule stigma. At sunset flowers open and anthers dehisce; flowers close <12 h later, typically before sunrise. Mature fruits are berry-like, with ~180 seeds per fruit. Senita cacti rely on the obligate pollinating seed-eating senita moth (*Upiga virescens* Hulst) for pollination, as senita is entirely self-incompatible and co-pollinators are typically unimportant (Holland and Fleming 2002).

Extrafloral nectar is produced from the tips of tepals on buds and flowers, and the tips of withered tepals on immature fruits. Such EFN associated with reproductive structures of senita cacti, and ant use of EFN, are illustrated in Fig. 2.1. In addition to EFN associated with reproductive structures, senita also have extrafloral nectaries just below areoles of new growth on stems, but extrafloral nectar production from these sub-areole nectaries usually occurs after the flowering season when new stem growth occurs. Extrafloral nectar production from tepals can vary within and among buds, flowers, and fruits, as well as with the relative size of such reproductive structures (S.A. Chamberlain and J.N. Holland, unpubl. data). Over a 24-hr time period, mean ± SE (range, *n*) secretion rates of extrafloral nectar for individual buds and immature fruit were 1.21 ± 0.32 µl (0-8.1, *n* = 31 plants) and 0.73 ± 0.20 µl (0-5.6, *n* = 31 plants), respectively. Over ~9 hrs for which flowers are open, secretion rates of extrafloral nectar were 0.84 ± 0.26 µl (0-3.3, *n* = 31 plants).
Buds and fruit are the dominant EFN resource, as flowers are only open for one night. Insects using EFN on senita include flies, beetles, and parasitoids, but ants are the most common consumers, including 12 species in three subfamilies at OPCNM: *Crematogaster depilis*, *C. larreae*, *Monomorium* sp., *Pheidole obtusospinosa*, *P. vistana*, *Solenopsis xyloni*, and *Tetramorium hispidum* (Myrmicinae); *Camponotus fragilis*, *C. ocreatus*, and *Myrmecocystus placodops* (Formicinae); and *Dorymyrmex insanus* and *Forelius mccooki* (or possibly *F. pruinosis*) (Dolichoderinae; Mackay and Mackay 2002). No ant species were observed to live on or within senita. All ants except *Forelius* were only active on senita after sunset (when flowers open). Buds, flowers, and immature fruit are all susceptible to a diverse range of herbivorous insects.

*Floral repulsion of ants* --- If flowers of senita cacti have chemicals that deter ants, then EFN resource supply may not mediate ant-flower interactions. We conducted behavioral assays to assess if flowers have ant repellents using similar protocols to Ness (2006). One hemisphere of petri dishes was a control and the other was wiped with a freshly opened senita flower. As pollen may be a source of ant repellency (Nicklen and Wagner 2006), we only used newly opened flowers with dehisced anthers. All petri dishes, flowers, and individual ants were used only once. We measured percent time spent in each hemisphere for 15 ants of each of four species (*Camponotus ocreatus*, *Crematogaster depilis*, *Forelius mccooki*, and *Pheidole obtusospinosa*) collected from multiple plants within an hour prior to the experiment. Ants were introduced to the petri dish immediately after dishes were wiped with flowers. After a 30 second acclimation period, ants were observed for 300 seconds. At 150 seconds, we rotated petri dishes 180° to account for any orientation effect. We used non-parametric (Wilcoxon) paired
difference tests (due to non-normal residuals) to examine whether the mean percent time in the floral hemisphere differed from the null hypothesis of 50%. We tested for differences among ant species using an ANOVA (SAS Institute 2004).

EFN-mediated ant-plant interactions — First, we conducted observational studies to examine whether EFN resources mediate the naturally occurring aggregative density of ants on plants and their interactions with flowers. On 28 randomly chosen plants for 14 census nights, we quantified the abundance of ants on plants, the proportion of flowers per plant that contained ants within flowers (ants consume EFN on the outside of flowers [see Fig. 2.1], so we only counted ants inside flowers), and the supply of EFN resources. The supply of EFN resources was estimated by the surrogate variable of the abundance of buds, flowers, and fruits. We censused three stems per plant as a proxy for whole plants, as thousands of buds, flowers, and fruits per plant were not feasibly countable (nor their EFN secretion rates measured). Flower number on the three stems was strongly correlated with whole plant flower number among the census nights ($n = 392, r = 0.42, P < 0.0001$). We recorded the proportion of flowers with ant species, but pooled species for analyses. Averaging among nights within plants to avoid pseudoreplication, we used simple linear regression to test whether the aggregative density of ants on plants varied with EFN resources, and the proportion of flowers with ants varied with EFN resources (SAS Institute 2004). Ant abundance, proportion of flowers with ants, and EFN resources were ln-transformed prior to analysis to meet assumptions of normality and homoscedacity.

Second, we experimentally tested if the aggregative density of ants on plants depended on the availability of EFN resources. We haphazardly chose two flowering
stems per plant \((n = 29\) plants\) with similar levels of EFN resources, as estimated by the number of buds, flowers, and fruit. We randomly assigned each stem to a control or EFN elimination treatment. Control stems were not manipulated, and we removed all buds, flowers, and fruit from EFN removal stems. Although removal of EFN with glue was the preferred protocol (Rudgers 2004), it was not feasible due to the large number of buds, flowers, and fruits. Treatments were established in the afternoon when ants were inactive on senita. Abundance of ant species was censused both diurnally and nocturnally on each of the two stems the day prior to experimental manipulation and for three days following. On the first day of the treatment, ants were censused once by day \((1830-1930\) hrs\) and four times by night \((2000, 2100, 2200,\) and \(2300\) hrs\). On the next two days, ants were censused once by day \((1830\) hrs\) and twice by night \((2000\) and \(2100\) hrs\). We used repeated-measures ANOVAs to test treatment effects on the aggregative density response of ants (PROC GLM, SAS Institute 2000). The first analysis was for the hourly time scale immediately following treatment establishment; the second was for the daily time scale. Ant species were lumped for statistical analyses; observations during censuses indicated that species responded similarly, such that statistical effects were not driven solely by the response of one abundant species. Ant abundance was In-transformed to meet statistical assumptions. Although analyses were performed on In-transformed abundance, for clarity we report results as percent change in ant abundance standardized to pre-manipulation ant abundance.

Third, we experimentally tested whether ant-flower interactions are mediated by EFN resources by randomly assigning two flowering stems per plant \((n = 23\) plants\) to a control or EFN removal treatment. We quantified EFN resources (buds, flowers, and
fruits) for the two stems prior to manipulation to assess any differences in pre-
manipulation resource levels on ant responses. Prior to ant activity on plants (1800 hrs),
all but one flower was removed from both control and EFN-removal stems; all buds and
fruit were also removed from EFN-removal stems. Each flower on control and EFN-
removal stems was observed for five minutes every 30 minutes for the two hours (2000-
2200) of peak flower visitation by senita moths (Holland and Fleming 1999). We
measured the time flowers were occupied by ants and the frequency of ant interactions
inside of flowers on control and EFN-removal stems. We summed data across five
minute time periods, as no differences occurred in response variables among time
periods. Due to lack of normality in the data, analyses were performed using non-
parametric (Wilcoxon) paired difference tests (SAS Institute 2004). We were unable to
examine ant species effects due to small sample sizes for individual species.

Ant effects on plant reproduction — We conducted ant exclusion experiments to
examine how ants influence plant reproduction through protection from herbivores and
interactions with flowers. Plant reproduction is predicted to increase with ants present
due to their deterrence of herbivores, but plant reproduction could also decrease due to
ant use of floral resources and their disruption of pollination. We established control and
ant exclusion treatments on each of 42 replicate plants. To improve our measure of
treatment effects and avoid idiosyncrasies of particular stems, we used multiple flowering
stems for each treatment (131 control and 150 ant exclusion stems among the 42 plants).
Although applying treatments to whole plants was the preferred design, it was not
logistically feasible and would have limited our sample sizes relative to a paired design.
We excluded ants with Tanglefoot (Tanglefoot, Grand Rapids, Michigan, USA) applied
to tape on the base of each stem. We did not apply tape to control stems, as prior study showed no tape effect on plant response variables (H. Passmore and J.N. Holland, unpubl. data). The effect of the exclusion treatment on ant abundance was examined twice during the experiment. Both analyses showed significant differences in ant abundance between control and exclusion stems (first census: control: 41.3 ± 7.2; exclusion: 5.9 ± 3.6; two-tailed paired t-test; \( t = 4.90, \) d.f. = 41, \( P < 0.0001 \); second census: control: 22.1 ± 5.5; exclusion: 7.6 ± 1.7; two-tailed paired t-test; \( t = 2.52, \) d.f. = 41, \( P = 0.016 \)). Although mean ant abundance on exclusion stems was not zero, this was largely driven by just a few stems on which ants gained access. On the first census of treatment effectiveness, 142 of 159 Tanglefoot stems (89%) had no ants on them whatsoever; 10 of the 17 stems that did have ants on them had less than 10 ants each. On the second census, 128 of 161 stems (80%) had no ants on them; 19 of the 33 stems that had ants on them had less than 10 ants each.

Senita's long flowering season allowed us to conduct several trials of this experiment for multiple plant reproduction variables. Multiple times throughout senita’s flowering season, a set of buds, flowers, and fruits were marked individually on control and treatment stems. Buds, flowers, and fruit of individual stems within each treatment of each plant were pooled in calculating each response variable, thereby treating plants as replicates instead of individual stems. Response variables included: bud survival (proportion of buds surviving to anthesis); fruit set (proportion of flowers initiating fruit 6 days after anthesis); immature fruit survival (proportion of set fruit surviving to mature fruit); fruit maturation (proportion of flowers surviving to 20 days after anthesis); flower-to-fruit longevity (age to which flowers and fruit survived); and seed production (seeds
per fruit). We also include unpublished results of a comparable experiment conducted at another site in another year (1998, Bahia de Kino, Sonora, Mexico; H. Passmore and J.N. Holland, unpubl. data). Senita do not appear to re-allocate resources among stems in response to experimental manipulations (Holland and Fleming 2002, Holland and Chamberlain 2007), which may have otherwise confounded our measures of plant reproductive response variables given the paired design of treatments within each individual replicate plant. Plant response variables (exclusion minus control) were analyzed with paired difference t-tests with plants as replicates. When parametric assumptions were not met, we used non-parametric (Wilcoxon) paired difference tests (SAS Institute 2004). Although our statistical inference is based on paired (exclusion minus control) differences, for clarity and ease of interpretation we present means and error estimates for the two treatments separately.

**RESULTS**

*Floral repulsion of ants* --- Flowers showed no obvious repulsive properties to four different ant species (Fig. 2.2). No ant species spent significantly more time in the control versus floral hemispheres of the behavioral assays (Wilcoxon paired difference test, d.f. = 15, \( P > 0.20 \) for each species). Moreover, time in control versus floral hemispheres did not differ among the four ant species (one-way ANOVA, \( F_{3,60} = 0.5493, P = 0.651 \)). Though not explicitly tested, observations of other ants in flowers on senita \((S. xyloni \text{ and } C. fragilis)\) which were not included in behavioral assays suggest they too were not averse. Thus, there were no obvious confounding effects of floral deterents on EFN resources mediating ant-flower interactions.
**EFN-mediated ant-plant interactions** --- Observational studies of naturally occurring ants on plants showed that their behavioral, aggregative density response increased with the supply of EFN resources (simple linear regression, $r^2 = 0.32$, $F_{1,26} = 12.1$, $P = 0.0018$; Fig. 2.3A). Although the aggregative density of ants on plants increased with EFN resources, observations of naturally occurring ant-flower interactions showed that ant use of floral resources, as measured by the proportion of flowers containing ants, decreased rather than increased with EFN resources (simple linear regression, $r^2 = 0.52$, $F_{1,12} = 12.9$, $P = 0.0037$; Fig. 2.3B). Of all ants observed in flowers, 4, 6, 7, 17, and 66% were *D. insanus*, *S. xyloni*, *Crematogaster depilis*, *Camponotus fragilis*, and *P. obtusospinosa*, respectively. The decrease in ant-flower interactions with EFN resources was not simply a result of variation in ant abundance among plants, as the proportion of flowers with ants was not related to ant abundance per plant (simple linear regression, $r^2 = 0.04$, $F_{1,12} = 0.42$, $P = 0.5288$).

Like the observational studies (Fig. 2.3A), experiments also showed that the aggregative density response of ants on plants was mediated by the availability of EFN resources (Fig. 2.4). The aggregative density of ants was unaltered on stems for which EFN remained intact. Yet, when EFN resources were eliminated, aggregative ant density on treatment stems decreased by 54% within hours of the manipulation ($F_{1,28} = 21.61$, $P < 0.0001$) and remained low for the following three days of observation ($F_{1,27} = 34.74$, $P < 0.0001$). There was a significant interaction between control and EFN-removal stems with time for both the hourly (Pillai’s trace = 0.53, $F_{3,26} = 9.88$, $P = 0.0002$; Fig. 2.4 inset) and daily analyses (Pillai’s trace = 0.54, $F_{3,25} = 9.92$, $P = 0.0002$; Fig. 2.4), indicating that the behavioral, aggregative density response of ants on plants was mediated by EFN.
resources. Damaging plants by removing reproductive structures with EFN may have activated the octadecanoid pathway and induced EFN secretion (Heil et al. 2001), thereby contributing to aggregative ant density on control versus EFN-removal stems. Yet, EFN secretion is likely not inducible, but rather constitutive, as EFN accumulates in the absence of ants and conspicuous herbivory (S. A. Chamberlain and J. N. Holland, unpubl. data). Thus, because EFN is secreted constitutively, removing buds, flowers, or fruits did not likely induce EFN secretion (cf. Heil et al. 2004). Moreover, if the aggregative density response of ants on plants resulted from induced EFN production through plant damage, then we should have seen increases in ants on control stems, which we did not (Fig. 2.4).

Experimental studies also support EFN resources mediating antagonistic ant-flower interactions (Fig. 2.5). In comparing ant interactions with flowers for stems with and without EFN resources, ants showed a greater use of floral resources when EFN resources were removed. Ants occupied flowers for longer time periods on stems without EFN resources compared to stems with EFN resources (Wilcoxon paired difference test, \( Z = 51.5, \text{d.f.} = 22, P = 0.036; \) Fig. 2.5A). Ants also interacted more frequently with flowers on stems without EFN resources compared to flowers on stems with EFN resources (Wilcoxon paired difference test, \( Z = 50.0, \text{d.f.} = 22, P = 0.023; \) Fig. 2.5B). Increased time spent in flowers and increased ant-flower interactions for stems without EFN resources occurred despite the aggregative density of ants decreasing on stems without EFN resources (Wilcoxon paired difference test, \( Z = -113, \text{d.f.} = 23, P < 0.0001; \) Fig. 2.5C). These results were not confounded by the pre-manipulation differences in the supply of EFN resources between control and treatment stems, as no significant
difference occurred (0.04 ± 4.84) between them prior to manipulation (two-tailed paired t-test, \( t = -0.0086, \) d.f. = 23, \( P = 0.993; \) Fig. 2.5D). Thus, the supply of EFN resources increases the aggregative density of ants on plants while simultaneously reducing ant-flower interactions.

*Ant effects on plant reproduction* --- In 2006 for the OPCNM population, seed production did increase in the presence of ants in one trial, but sample size was small (\( n = 8 \)). Yet, the other trial with a larger sample size (\( n = 37 \)) showed no effect on seed production. In 1998 for the Bahia de Kino population, ant exclusion increased fruit maturation, suggesting that ant-flower interactions can reduce plant reproduction (Table 2.1). Even though the particular plant responses to ants in certain years and populations of study did occur, ants did not have an overwhelming effect on plant reproduction, either through plant protection or ant-flower interactions, as no effects were observed on bud survival, fruit set, fruit survival, fruit maturation, or flower-to-fruit longevity (Table 2.1). Thus, ants did not appear to have sustained mutualistic or antagonistic effects on plants, though certain years and populations did show that plant reproduction can be altered via herbivore protection and ant-flower interactions.

**DISCUSSION**

Recognition that both predation and competition are consumer-resource interactions has provided a mechanistic basis for understanding the consequences of interspecific interactions for the dynamics of ecological systems (Tilman 1982, Murdoch et al. 2003, Turchin 2003). Species interactions are often mediated by the interplay between resource supply and consumer density, and the supply of and a consumer's
density response to one resource may in turn yield context dependent use of other resources. The point has generally been missed, however, that mutualism is also a consumer-resource interaction (Holland et al. 2005). We studied interactions between a guild of ants and extrafloral nectar (EFN) bearing senita cacti to examine how the supply of one resource mediates a consumer's density response and its context dependent use of another resource. Specifically, we examined how the supply of EFN resources mediates the behavioral, aggregative density response of ants on plants, and in turn whether ant use of floral resources is context dependent upon floral chemical deterrents, EFN resource supply, and density responses of ants. Even though empirical support occurs for each of floral deterrents (e.g., Ghazoul 2001), EFN-mediated ant-plant protection (e.g., Bronstein et al. 2006), and EFN-mediated use of floral resources by ants (e.g., Ness 2006), studies have not examined the context dependency of each of them on one another. This is despite the fact that EFN-mediated distraction of ants from floral resources may be contingent upon floral chemical deterrents, and that EFN-mediated ant-plant protection interactions may simultaneously mediate ant use of floral resources.

First, and possibly foremost, the context dependent use of EFN and floral resources by ants may be contingent on whether flowers have properties that deter and repel ants (Ghazoul 2001). Moreover, ant species may vary in their deterrence from flowers by floral chemical deterrents (Ness 2006). Our behavioral assays showed no indication that senita cacti had floral properties that deterred any of multiple ant species from using them as resources (Fig. 2.2). Because ant-flower interactions were not contingent upon floral chemical deterrents, consumer-resource interactions between ants and floral resources may be mediated by the supply of EFN resources. In the senita
system, ant-flower interactions can be particularly detrimental for plant reproduction by disrupting their sole, obligate pollinator, whose peak flower visitation coincides with nocturnal ant activity (Holland and Fleming 1999).

The supply of EFN resources by plants did mediate the behavioral, aggregative density response of ants on plants (Figs. 2.3A, 2.4, and 2.5C) and their interactions with flowers (Figs. 2.3B, 2.5A,B). The aggregative density response of ants on plants increased with the supply of EFN resources, but this did not increase ant-flower interactions. Instead, ant-flower interactions decreased with the supply of EFN resources, which likely satiated and distracted ants from floral resources. However, when EFN resources were absent, ant interactions with flowers and the duration of those interactions increased compared with when EFN resources were available. Thus, ant use of floral resources did not appear to be context dependent upon the aggregative density of ants on plants, as ant-flower interactions did not increase with the density of ants on plants. In fact, ant interactions with flowers increased on plant stems without EFN resources despite their aggregative density decreasing compared to stems with EFN resources (Fig. 2.5). In this regard, ant use of floral resources was context dependent on the supply of EFN resources. Hence, the aggregative density response of ants on plants was mediated by, and context dependent upon, the supply of EFN resources. To this end, the supply of EFN resources can mediate the potential for both mutualistic ant-plant interactions and antagonistic ant-flower interactions by increasing the aggregative density response of ants protecting plants, while simultaneously reducing ant use of floral resources.

Interactions between ants and EFN-bearing plants are often mutualistic, as EFN is a food resource that attracts and rewards ants that in turn protect plants from herbivory.
(Bronstein et al. 2006). However, ants also often exploit floral resources (e.g., Galen 1983), which commonly leads to antagonistic ant-plant interactions through their interference with plant reproduction and pollination processes (e.g., Ness 2006).

Although we did not explicitly quantify ant effects on herbivores and pollinators, our ant exclusion studies are consistent with ants increasing plant reproduction through plant protection and decreasing plant reproduction through disruption of pollination, depending upon the particular year and population of study (Table 2.1). Note that all plant reproduction variables in Table 1 relate to female fitness, and male fitness variables may also be affected by ants, as ants are known to reduce pollen viability when they contact dehisced anthers (Nicklen and Wagner 2006). While we did not quantify the effects of ants on male fitness, ants did not show any sustained positive or negative effects on female fitness as measured through multiple plant reproductive variables. In addition, it is worth noting that, as with any ant-plant study employing tanglefoot, such an ant exclusion treatment may also affect herbivore access to plants, though we do not suspect this confounds the lack of significant effects of ants on plant reproduction. Flightless herbivores do indeed feed on senita, but most herbivores can access senita in the presence of tanglefoot. Despite these caveats and the pronounced effects of EFN resources in mediating the aggregative density of ants on plants and their interactions with flowers, consumer-resource interactions between ants and plants were largely commensalistic.

Other studies have shown great spatio-temporal variation in and context dependency of mutualistic interactions of EFN-mediated ant-plant interactions (Horvitz and Schemske 1990, Rashbrook et al. 1992, Bronstein 1994, Zachariades and Midgley 1999, Wirth and

In our studies, EFN resources did mediate the aggregative density response of ants on plants and their interactions with floral resources, such that interplay between resource supply and consumer density of potentially mutualistic interactions can indeed be crucial to the ecological consequences of their interspecific interactions. Other consumer-resource systems that are often mutualistic may too depend critically on the supply of resources, and often mutualistic consumers may become commensalistic or antagonistic by exploiting their partners beyond those resources supplied as mutualistic rewards, like that of ant use of floral resources of senita cacti. For example, hemipterans (e.g., coccids, aphids) produce food excretions consumed by ants. In tending hemipterans and consuming food excretions, ants protect them from natural enemies. Depending on hemipteran excretion rates, ant density, and among other factors hemipteran density, ants can shift to consuming individuals rather than tending them and only consuming their excretions, thereby leading to commensalistic or antagonistic ant-hemipteran interactions (Stadler and Dixon 2005). Similarly, lycaenid caterpillars produce food secretions that attract and reward ants in exchange for their protection from natural enemies. Yet, ants may go beyond consuming the food secretions produced by lycaenid larvae to eating individual larva (Pierce et al. 2002). Thus, consumer-resource interactions comprised of typically mutualistic consumers may be prone to conditional outcomes depending on the supply (and quality) of resources provided as mutualistic rewards. The supply of resources may be critical to the establishment of other consumer-resource mutualisms. For example, the quantity and constituents (sugars, amino acids) of floral nectar and
pollen resources of plants can be key in determining which pollinators interact with which plants (Potts et al. 2003). Likewise, ambient levels of soil nutrients (e.g., phosphorus, nitrogen) and their supply rate to plants by mycorrhizae or rhizobia may be crucial in the establishment of plant-microbial mutualisms (Douglas 1994, Smith and Read 1997). Although these and many other interactions are often consumer-resource mutualisms, they may become antagonistic if the consumer exploits a species beyond those resources supplied as mutualistic rewards, which may commonly depend on the supply of the reward resource and density responses of consumers to them.

In sum, our results have shown that resource supply and consumer density responses of potentially mutualistic interactions, like that of predator-prey and competitive interactions, can be crucial contextual factors in mediating their interspecific interactions. Examining mutualisms through the lens of consumer-resource interactions can lead to otherwise unrecognized principles more commonly appreciated in predator-prey and competitive systems. Indeed, context dependency is increasingly a central component of understanding the strengths, outcomes, and dynamics of species interactions (Agrawal et al. 2007). Explicitly considering the supply rates of resources provisioned by one mutualist and a consumer's density response to them may provide new insights into the well-established context dependency and conditionality of mutualistic interactions (Bronstein 1994).

ACKNOWLEDGMENTS

We thank David Guitierrez, Katherine Horn, Pamela Thompson, and Aline Waguespack for field and laboratory assistance, and the National Park Service and Organ
Pipe Cactus National Monument for logistical support. P. Ward assisted in the
identification of ants. S. Emery, J. Rudgers, and K. Whitney provided helpful comments
on this study. S.A.C. was supported by a Wray Todd Fellowship.

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Table 2.1. Mean (± SE) effects of control and ant exclusion treatments for six plant reproductive variables (see Methods for description of variables). P-values are for paired-difference tests using mean difference between treatments (plants as replicates), with a null hypothesis of zero. Sample sizes given are number of plants, and vary among response variables as we were not able to quantify variables for some plants.

<table>
<thead>
<tr>
<th>Plant Variable</th>
<th>n</th>
<th>Control</th>
<th>Ant Exclusion</th>
<th>P†</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Bud Survival</strong> (proportion)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1998</td>
<td>18</td>
<td>0.65 ± 0.04</td>
<td>0.62 ± 0.03</td>
<td>0.59</td>
</tr>
<tr>
<td>2006</td>
<td>23</td>
<td>0.64 ± 0.05</td>
<td>0.71 ± 0.04</td>
<td>0.16</td>
</tr>
<tr>
<td><strong>Fruit Set</strong> (proportion)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2006, trial 1</td>
<td>36</td>
<td>0.20 ± 0.03</td>
<td>0.22 ± 0.03</td>
<td>0.61</td>
</tr>
<tr>
<td>2006, trial 2</td>
<td>9</td>
<td>0.22 ± 0.04</td>
<td>0.18 ± 0.07</td>
<td>0.63</td>
</tr>
<tr>
<td><strong>Immature Fruit Survival</strong> (proportion)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2006</td>
<td>21</td>
<td>0.68 ± 0.06</td>
<td>0.62 ± 0.08</td>
<td>0.58</td>
</tr>
<tr>
<td><strong>Fruit Maturation</strong> (proportion)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1998</td>
<td>9</td>
<td>0.78 ± 0.04</td>
<td>0.86 ± 0.04</td>
<td>0.03</td>
</tr>
<tr>
<td>2006, trial 1</td>
<td>36</td>
<td>0.12 ± 0.02</td>
<td>0.13 ± 0.02</td>
<td>0.81</td>
</tr>
<tr>
<td>2006, trial 2</td>
<td>19</td>
<td>0.71 ± 0.03</td>
<td>0.75 ± 0.05</td>
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<tr>
<td><strong>Flower-to-Fruit Longevity</strong> (days)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2006</td>
<td>36</td>
<td>5.70 ± 0.53</td>
<td>5.85 ± 0.58</td>
<td>0.86</td>
</tr>
<tr>
<td><strong>Seed Production</strong> (number of seeds)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2006, trial 1</td>
<td>8</td>
<td>188.3 ± 21.3</td>
<td>145.0 ± 25.3</td>
<td>0.01</td>
</tr>
<tr>
<td>2006, trial 2</td>
<td>37</td>
<td>159.1 ± 8.5</td>
<td>154.3 ± 7.5</td>
<td>0.54</td>
</tr>
</tbody>
</table>

†Parametric paired difference t-tests used in all cases, except "Seed Production 2006, trial 1", in which a non-parametric (Wilcoxon) paired difference test was used.
Figure 2.1. Extrafloral nectar production, and ant consumption thereof, associated with buds, flowers, and immature fruit of senita cacti. Droplets of extrafloral nectar emerging from the tips of tepals of multiple buds (a) and a single magnified bud (b). Individuals of *Crematogaster* consuming nectar from the tips of tepals on an immature fruit (c) and at the base of an open flower (d). Photo credit: J.N. Holland.
Figure 2.2. Mean (± SE) percent time that four ant species spent in the floral hemisphere of the ant behavioral assays to potential floral deterrents of flowers. The null hypothesis of no preference (50%) for the control vs. floral hemisphere of petri dishes is depicted by a dashed line. Bars sharing the same letter are not significantly different (Tukey HSD test). C. ocreatus = *Camponotus ocreatus*; C. depilis = *Crematogaster depilis*; F. mccooki = *Forelius mccooki*; P. obtusospinosa = *Pheidole obtusospinosa*.
Figure 2.3. Mean ant abundance per plant (A) and mean proportion of flowers with ants in them (B) as a function of the quantity of EFN resources (simple linear regression with 95% confidence bounds). Each data point is a mean of 14 census dates for each of 28 plants (A), and a mean of 28 plants for each of 14 census dates (B). All variables were ln-transformed prior to analysis and are presented as ln-transformed values here. Note, these results should be interpreted as a qualitative (i.e., positive) relationship between ant abundance and EFN resources, rather than specific functional responses given that data are averages among nights and plants.
Figure 2.4. Proportion change in ant abundance (mean ± SE) over four days on control and experimentally reduced EFN stems. Jun-18 is pre-manipulation, and hence the standard reference point for proportion change. Inset represents change on an hourly time scale of the night immediately following the afternoon manipulation.
Figure 2.5. Ant response to EFN reduction as an experimental test of the distraction hypothesis. Although a paired design, separate means (± SE) for control vs. EFN reduction are presented (n = 23 plants for all comparisons) for, (A) time (seconds) ants spent in flowers once ants entered flowers; (B) number of times ants contacted flowers; (C) ant abundance post-manipulation, during the experiment; and (D) pre-manipulation EFN resource levels. *P < 0.05; ns, non-significant.