

UC San Diego

UC San Diego Electronic Theses and Dissertations

Title

Pollinator harassment in a protection mutualism: effects of the Argentine ant on coast barrel cactus reproductive success

Permalink

<https://escholarship.org/uc/item/8vr4m92g>

Author

McCann, Kyle R.

Publication Date

2012

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA, SAN DIEGO

**Pollinator harassment in a protection mutualism: effects of the Argentine ant on coast
barrel cactus reproductive success**

A thesis submitted in partial satisfaction of the requirements

for the degree Master of Science

in

Biology

by

Kyle R. McCann

Committee in charge:

Professor David A. Holway, Chair
Professor Joshua R. Kohn
Professor James Nieh

2012

Copyright

Kyle R. McCann, 2012

All rights reserved

This thesis of Kyle R. McCann is approved, and it is acceptable in quality and form for publication
on microfilm and electronically:

Chair

University of California, San Diego

2012

DEDICATION

This thesis is dedicated to my beautiful wife Sandy and my amazing son Aiden. I know I am blessed every day to have them in my life.

EPIGRAPH

“Science is a way of thinking much more than it is a body of knowledge.”

-Dr. Carl Sagan

TABLE OF CONTENTS

Signature Page.....	iii
Dedication.....	iv
Epigraph.....	v
Table of Contents.....	vi
List of Figures.....	vii
List of Tables.....	viii
Acknowledgements.....	ix
Abstract.....	x
Introduction.....	1
Methods.....	4
Results.....	7
Discussion.....	11
References.....	21

LIST OF FIGURES

Figure 1: Ants in flowers.....	14
Figure 2: Floral visitation rates by pollinator type.....	15
Figure 3: Mean duration of floral visits by ants in flowers.....	16
Figure 4: Mean duration of floral visits by pollinator type.....	17
Figure 5: Seed number per fruit.....	18
Figure 6: Bees absence and its effect of seed number per fruit.....	19

LIST OF TABLES

Table 1: Pollinator survey cactus characteristics.....	20
--	----

ACKNOWLEDGEMENTS

I would like to thank my committee chair, Dr. David Holway. His insights, vast knowledge of flora and fauna and scientific guidance have been invaluable.

I would like to thank Dr. Josh Kohn and Dr. James Nieh for serving on my committee. Their participation is much appreciated.

I would like to thank the members of my lab: Dr. Ho Jung Yoo, Dr. Erin Wilson, Katie Levan, Brian Park and James Hung. Their help in all aspects of the project were instrumental. I appreciate all the help, insights, ideas and support.

I would also like to thank the Cactus and Succulent Society of America and the Marc David Belkin scholarship for their generous support of my research over the past two years.

And most importantly I would like to thank my wife for giving my overwhelming support over the two years of my thesis research. These two years have been the craziest of my life and I do not know what I would have done without her.

ABSTRACT OF THESIS

Pollinator harassment in a protection mutualism: effects of the Argentine ant on coast barrel cactus reproductive success

by

Kyle R. McCann

Master of Science in Biology

University of California, San Diego 2012

Professor David A. Holway, Chair

In this study we have examined a food-for-protection mutualism and its invasion by the Argentine ant (*Linepithema humile*). The San Diego Barrel Cactus (*Ferocactus viridescens*) produces extrafloral nectar to attract ants, which in turn deter herbivores. By utilizing both invaded and uninvaded sites, we examined the effects of Argentine ant invasion on cactus reproductive output (seedset) and pollinator visitation. Argentine ants were found in flowers at a much higher rate than native ants in our system and cacti tended by the most prominent native ant in our system, *Crematogaster californica*, were found to have increased seed set (when controlling for fruit number) when compared to Argentine ant tended cactus. This result may be due to pollen limitation as pollinators (96% of which were bee spp.) spent significantly less time in flowers of cacti tended by *L. humile*. Thus invasion by an aggressive cacti-tending ant

may have long term effects on its host plants by shifting the rewards and consequences of an previously established food-for-protection mutualism.

INTRODUCTION

Introduced species that create novel associations with other organisms can shift mutualisms away from reciprocally beneficial interactions (Kiers et al 2010). Such changes may be especially likely when introduced species differ qualitatively or quantitatively from native mutualist partners. Pollination mutualisms seem of particular interest in this regard because they tend to be open interactions that are susceptible to exploitation by novel partners (Traveset & Richardson 2005). Plants can suffer fitness costs when pollination networks are altered by introduced species, such as novel pollinators or species affecting the behavior of native pollinators (Traveset & Richardson 2005).

Pollination mutualisms involving plants that produce extra-floral nectar (EFN) may be especially prone to a specific type of disruption, given that EFN attracts ants, which can simultaneously protect plants from herbivores but also interfere with pollinators (Ness 2006). In general, ant-plant protection mutualisms benefit plants that participate in the interaction (Chamberlain & Holland 2009), including cases where the tending ants are introduced species (Ness & Bronstein 2004). Ant protection, for example, can reduce herbivore damage and increase plant performance as a consequence (Chamberlain & Holland 2009). EFN production may also benefit plants through the distraction of ants away from sources of floral nectar, thus minimizing contact between ants and pollinators (Wagner & Kay 2002, Holland & Chamberlain 2008). Over evolutionary time, plants might be expected to adjust the level EFN production in accordance with costs associated with herbivory or pollinator interference. In cases where nectar-craving invasive ants are present, however, levels of EFN production that are shaped by the responses of native ants may lead to an increased occurrence of floral visits and a greater degree of pollinator interference (Lach 2003).

In this study we examine the importance of pollinator-interference in an EFN-bearing plant, the coast barrel cactus (*Ferocactus viredescens*) in coastal southern California. This cactus produces extrafloral nectar (EFN) attractive to ants, including the invasive Argentine ant (*Linepithema humile*), and ant protection discourages insect herbivores from feeding on cacti (Ludka 2008). In addition to patrolling extrafloral portions of cacti, ants also visit flowers (Ludka 2008), where they could potentially interfere with pollinators and reduce cactus seed set as a consequence, as in the case of *Ferocactus wislizenii* tended by native fire ants (Ness 2006). Ant-pollinator interactions might be especially likely on cacti controlled by the Argentine ant, which is a species that favors carbohydrate-rich resources (Way 1963, Holway et al. 2002) and often forages for nectar in flowers where it tends to displace legitimate floral visitors (Blancafort & Gomez 2005, Lach 2005, 2007, & 2008).

Here we collate three years of survey data documenting floral visitation by ants and the seed set of cacti either controlled by the Argentine ant or by *Crematogaster californica*, the most prevalent native ant in the system. These data are combined with a one-year survey of bee pollinators on the same set of cacti. Using these surveys, we test whether or not floral visitation by ants affects pollinator visitation and, if so, the degree to which such changes affect the reproductive success of cacti. This system provides a rare opportunity to examine how a novel mutualist partner affects the balance between plant protection and pollinator interference. Relatively few studies on mutualisms make explicit comparisons between native and introduced ants with respect to how each performs as a mutualist partner (Ness & Bronstein 2004). Because barrel cacti are typically controlled by a single ant species at a time (Morris et al. 2006,

Ness et al. 2006, Ness 2006, Ludka 2008), it is possible to link floral visitation by ants to variables directly related to plant fitness through interactions between ants and pollinators.

METHODS

Study System

A patchily distributed and uncommon species, *Ferocactus viridescens* is restricted to coastal sage scrub on well-drained slopes in coastal San Diego County, CA and northwestern Baja California (Ingram 2008). We studied *F. viridescens* along a 15-km stretch of coastline in San Diego Co. from Kate O Sessions Memorial Park in the south to the Torrey Pines State Reserve in the north. The coast barrel cactus produces extrafloral nectar (EFN) during the winter, spring and summer. Cacti bloom from April through June and produce fruit from July into early fall. EFN attracts a variety of ant species, including the invasive Argentine ant (*Linepithema humile*) (Ludka 2008). As many as 18 native ant species visit coast barrel cacti, but ant diversity is greatly reduced in areas invaded by *L. humile* (Glenn & Holway 2008, Ludka 2008). The study area is presently a mosaic of sites occupied by native ants and sites invaded by the Argentine ant (Glenn & Holway 2008, Ludka 2008).

As part of an earlier study (Ludka 2008), we monitored 37 cacti in 2007 and 48 cacti in 2008 that were controlled by either *L. humile* (n = 32) or by *C. californica* (n = 16). These cacti were visited weekly to determine patterns of ant visitation and to estimate several measures of female reproductive success (Ludka 2008). In 2010 we selected 48 plants from the 2008 survey and again monitored them at weekly intervals during the spring and early summer to quantify ant and bee visitation to flowers. With respect to the ants in control of cacti, the distribution of the Argentine ant remained relatively static during the four-year period of the study; this aspect of the study system allowed us to classify individual cacti as controlled by either *L. humile* or *C. californica*. A cactus was considered controlled by a given ant species if it was occupied by that species on more than 50% of survey visits. Cacti controlled by either *L. humile* or *C. californica*

were spatially interspersed to the fullest extent possible throughout the study area and did not differ from one another in their volume, blooming period, or number of buds, flowers or fruit (Table 1).

Pollinator surveys

We conducted pollinator surveys in 2010 on the set of 48 focal cacti described in the previous section to determine if the presence of ants in flowers has any effect on the type of pollinators that visit flowers, the frequency of their visits, or the length of their visits. Each cactus was visited weekly from April through June, and pollinator data were collected if a cactus had at least one flower open. During each visit to a cactus, we spent a 5-min watching for pollinators and collected the following data: type of pollinator, duration of each floral visit (from landing to take off), whether or not ants were present on the cactus (and if so how many), and whether or not ants were present in flowers (and if so how many). A potential pollinator was considered to have “visited” a flower if it remained there for at least 5 s. The vast majority (96.3%) of potential pollinators in our system were bees, which we divided into three categories: cactus bees (*Diadasia* sp. 1 and sp. 2 are not reliably identified in the field; cactus bees are thus hereafter referred to as *Diadasia*), European honeybees (*Apis mellifera*), and small native bees (numerous morphospecies of halictids).

Cactus seed set

In 2007, 2008 and 2010, we estimated seed set for sample fruit collected from cacti controlled by either *L. humile* or *C. californica*. Fruit were collected in the fall of each year, once they had ripened. A sample of 1 -3 fruit was carefully removed from each cactus and placed in a drying oven for one week to remove moisture. From each fruit, all of the seeds and a subset of 100 seeds were then weighed. The weight of 100 seeds was then used to estimate mean mass

per seed and total seed number per sample fruit. Seed number per sample fruit (averaged across fruit for samples with > 1 fruit per cactus) was the variable used in all analyses concerning the female portion of cactus reproductive success. Statistical comparisons involving seed number per sample fruit consider yearly values and also time-averaged values for those individual cacti for which we have > 1 year of ant visitation data and for which ant occupancy remained consistent over time. Values averaged over time integrate long-term effects of sustained ant presence on cacti.

RESULTS

Presence of ants in cactus flowers

Patterns of ant visitation varied among years and depending on whether *C. californica* or *L. humile* controlled cacti. Compared to *C. californica*, *L. humile* occurred more often in flowers in 2010 (G-test: $G^2 = 4.53$, $p = 0.03$) and across years (G-test: $G^2 = 4.23$, $p = 0.04$), but not in 2007 (G-test: $G^2 = 0.981$, $p > 0.05$) or 2008 (G-test: $G^2 = 0.08$, $p > 0.05$). Ant visitation in flowers was very low during the 2008 blooming period, which followed a winter in which precipitation was well below normal and ant activity was relatively low in this system (Ludka 2008).

The presence or absence of *L. humile* in cactus flowers depended on the number of ants on the cactus itself. Cacti in which ants were observed at least once in flowers during the 2010 survey had, on average, $6.2 (\pm 0.8)$ ants on them, not including those in the flowers, compared to $1.5 (\pm 0.3)$ ants on cacti for which ants were never observed in flowers (two-sample t-test: $t = 5.89$, $df = 30$, $p < 0.0001$). Other measured cactus variables were unrelated to whether or not the Argentine ant visited flowers. For example, cacti in which *L. humile* was observed at least once in flowers were neither larger nor did they have more flowers compared to cacti on which this species was never observed in flowers (two-sample t-tests: $p > 0.05$ for both comparisons).

Pollinator surveys

Irrespective of whether cacti were controlled by the Argentine ant or by *C. californica*, the most commonly observed floral visitors were cactus bees, *Diadasia*, which we observed visiting 60.4% (29/48) of cacti in the 2010 pollinator survey. In comparisons between cacti controlled by *L. humile* or by *C. californica*, there was no difference in the proportion of cacti on which *Diadasia* were observed versus those for which they were not (Chi-square test: $p > 0.05$). Moreover, on cacti where we did observe *Diadasia*, the number of floral visits by these bees did

not differ between cacti controlled by *L. humile* versus those controlled by *C. californica* (Fig. 2; two-sample t-test: $t = 0.13$, $df = 27$, $p = 0.897$).

Compared to *Diadasia*, other bees visited fewer cacti. We observed *Apis* visiting flowers of 27.1% (13/48) of the cacti in the survey and, as with *Diadasia*, the species of ant in control of the cactus had no effect on whether or not *Apis* was observed on that cactus (Chi-square test: $p > 0.05$) or the number of floral visits by this species on cacti where we did observe *Apis* (Fig. 2; two-sample t-test: $t = 1.63$, $df = 11$, $p = 0.131$). We observed small native bees on 18.8% (9/48) of the cacti in the survey, and these bees occurred more often on cacti controlled by *C. californica* (7/16) than on cacti controlled by *L. humile* (2/32) (Chi-square test: $\chi^2 = 7.54$, $df = 1$, $p = 0.006$). On those cacti where we observed small native bees, however, the number of floral visits by this class of pollinator did not differ for cacti controlled by *L. humile* versus those controlled by *C. californica* (Fig. 2; two-sample t-test: $t = 0.42$, $df = 7$, $p = 0.686$). Comparisons of overall rates of visitation on those cacti visited by each type of bee revealed that *Apis* visited cactus flowers less often compared to *Diadasia* and small native bees, which did not differ from one another in their rate of visitation (One-way ANOVA: $F_{2,48} = 4.086$, $p = 0.0230$; Fisher's PLSD with $\alpha = 0.05$). In this latter analysis, data were pooled with respect to the type of ant in control of the cactus for each type of bee separately.

The presence of ants in flowers reduced the duration of floral visits by bees. For all bees combined, for example, the mean duration of floral visits decreased with the proportion of survey visits during which time we observed ants in flowers (Fig. 3). For those cacti in which ants were never observed in flowers, the mean duration of floral visits by bees did not differ between cacti controlled by *L. humile* versus those controlled by *C. californica* (two-sample t-test: $t = 1.75$, $df = 15$, $p = 0.10$).

To isolate which type of bee contributed to the pattern illustrated in Figure 3, we compared the duration of floral visits by different bees between cacti controlled by *L. humile* and cacti controlled by *C. californica*. Floral visits by cactus bees were nearly twice as long, on average, on cacti controlled by *C. californica* compared to those controlled by *L. humile* (Fig. 4; two-sample t-test: $t = 3.024$, $df = 23$, $p = 0.006$). Although sample sizes for comparisons involving the other types of bees were small, the duration of their visits did not appear to depend as strongly on the type of ant in control of the cactus (Fig. 4; two-sample t-test for *Apis*: $t = 0.164$, $df = 7$, $p = 0.875$; two-sample t-test for small native bees: $t = 0.684$, $df = 6$, $p = 0.519$). Pooling data on the mean duration of visits for different bee types revealed that floral visits by all bees were over twice as long, on average, at cacti controlled by *C. californica* compared to those controlled by the Argentine ant. This comparison held for the mean duration of all bee visits combined (two-sample t-test: $t = 2.56$, $df = 44$, $p = 0.014$; 18.8 ± 3.33 versus 8.44 ± 2.31 seconds) and also for the mean duration of just native bees (two-sample t-test: $t = 3.47$, $df = 44$, $p = 0.001$; 17.27 ± 2.66 versus 6.00 ± 1.85 seconds).

Cactus seed set

Although values in every year did not always reach statistical significance, cacti controlled by the Argentine ant consistently set fewer seeds per sample fruit compared to cacti controlled by *C. californica* (Fig. 5). Data for 2010 and mean data for those individual cacti for which we have > 1 year of ant visitation data revealed that cacti tended by *L. humile* set significantly fewer seeds (per sample fruit) compared to cacti tended by *C. californica* (Fig. 5). Seed number per sample fruit was also enhanced by bee visitation, at least for those cacti controlled by *C. californica*, which experienced longer visits by cactus bees (Fig. 4) and by all bees combined. For cacti controlled by *C. californica*, for example, seed number per sample fruit

was over two times higher when bees were observed visiting cactus flowers compared to those cacti for which we did not observe bees (Fig. 6).

DISCUSSION

The results of this study illustrate how patterns of pollinator visitation on an EFN-bearing plant change as a result of ant invasion. Compared to cacti controlled by the most prevalent native ant in our system, cacti controlled by the invasive Argentine ant were more likely to have ants foraging inside of flowers (at least in some years), were visited for shorter lengths of time by cactus bees (*Diadasia*), the most common pollinator of cacti, and set fewer seeds per sample fruit (at least in some years). The importance of bees as pollinators in this system is underscored by the fact that cacti where we observed bees set more than twice as many seeds per sample fruit compared to cacti where we saw no bees, at least in areas still occupied by native ants.

Floral visitation by the Argentine ant and the accompanying displacement of floral visitors are now known from a number of systems (Visser et al. 1996, Lach 2007, Blancafort & Gomez 2005, and Lach 2008). The mechanisms responsible for the displacement of floral visitors are not clearly known in any of these systems, but direct interference and reduction or modification of floral rewards are all possibilities. Although Argentine ant workers are relatively small, they aggressively interact with arthropods exceeding them in size (Holway 1999), and we have observed individual *L. humile* workers lunging at and driving off *Diadasia* and other native bees from cactus flowers. Compared to eusocial bees, such as *Apis*, *Diadasia* and the other solitary bees that visit coast barrel cactus flowers may be more averse to potential ant threats in flowers given the ultimate consequences of injury or death to their fitness. Because *L. humile* seldom occurs in the flowers of the coast barrel cactus in large numbers, exploitation of floral nectar to levels that would discourage pollinators from lingering in flowers seems like an unlikely explanation for the reduced duration of cactus bee visits.

Although floral visitation by the Argentine ant commonly occurs (Blancafort & Gomez 2005, Lach 2005, 2007, 2008, Junker et al. 2011), we know of only one other published study that reports negative consequences to the host plant. Blancafort & Gomez (2005) found that fruit set and seed set for the shrub *Euphorbia characias* were lower in an area invaded by the Argentine ant compared to an adjacent area occupied by native ants. In the present study seed number per sample fruit was significantly lower for Argentine ant controlled cacti compared to cacti controlled by *C. californica* in 2010 (and averaged across time) but not in 2007 or 2008. The discrepancy between 2010 and earlier years may stem from 2010 being a better year for cactus reproduction in terms of overall fruit production compared to earlier years. Reduced seed set is consistent with reduced bee visitation as documented in this study (see also Ness 2006). Unlike Blancafort & Gomez (2005), we did not detect any differences in fruit set as a function of the ant in control of the cactus.

Mutualisms are often seen as mutually beneficial interactions, interactions in which each species reciprocal benefits from the partner species. What is becoming increasingly understood is how highly complex and behaviorally dynamic these relationships are (Bronstein 1994). Our study has demonstrated how dynamic and context dependent these mutualistic interactions can be. In our system, Argentine ants are lowering the fitness of their host plant, *Ferocactus viridescens*, by shortening the visitation length of the most common flower visitor *Diadasia*. The reduced seed set associated with these shorter visits could be caused by pollen limitation, thus reducing the quality of quantity of pollen being delivered to flowers on pollinator visits. How quickly can a host plant adapt to an invasive mutualistic partner is yet to be seen. Will *Ferocactus viridescens* shift resources away from EFNs? If shifts do occur, how will they affect the protection services provided by ants in the food-for-protection mutualism? As

the mechanisms for the introduction of invasive species increase (increasingly fragmented habitats, globalization, commerce, etc.) how will mutualism participating species respond to the novel partner species. Long term studies will be needed to monitor the response (or lack thereof) to these increasingly dynamic mutualistic relationships.

Figure 1

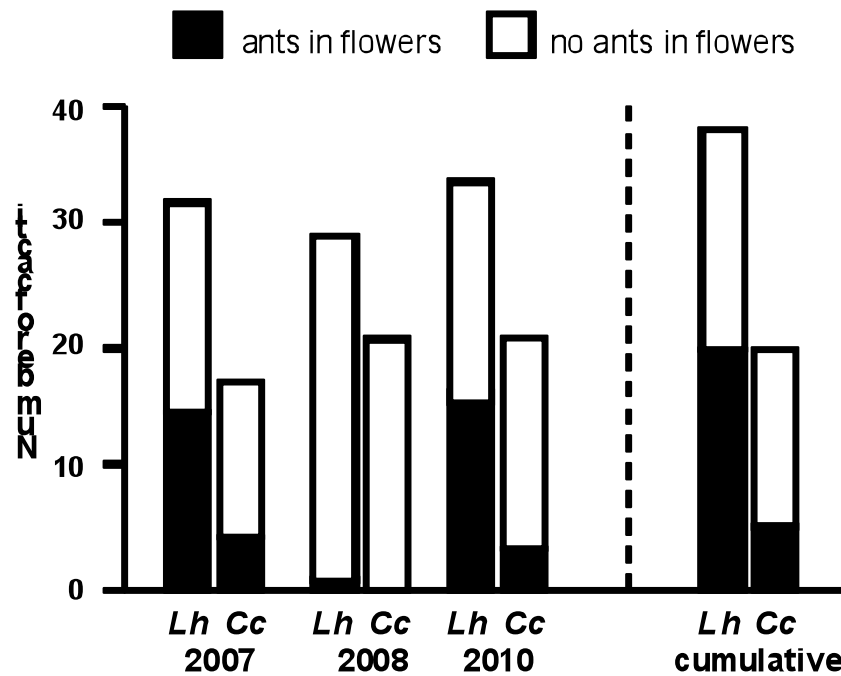


Figure 1. Ant presence or absence in flowers of coast barrel cacti controlled by either *Linepithema humile* (Lh) or *Crematogaster californica* (Cc). An individual cactus was considered to have ants present in its flowers if at least one ant was observed inside an open flower during at last one survey in a given year (2007, 2008, or 2010). The “cumulative” category illustrates the extent of ant visitation for individual cacti monitored in more than one year.

Figure 2

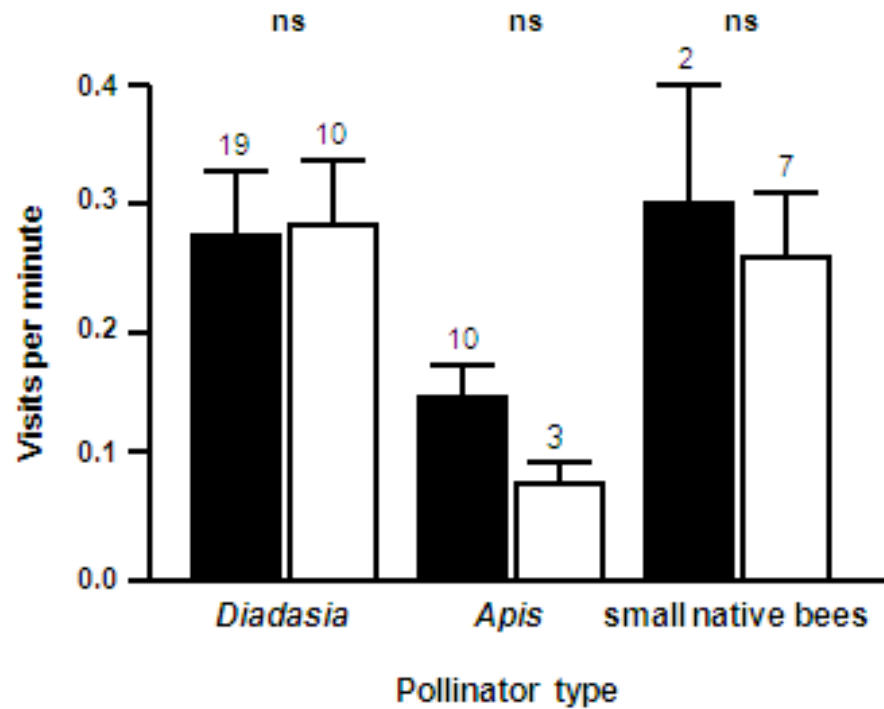


Figure 2. The mean (\pm SE) number of floral visits per minute of observation for *Diadasia*, *Apis mellifera*, and small native bees. Open bars show cacti controlled by *Crematogaster californica*; closed bars show cacti controlled by *Linepithema humile*. Each data point represents the number of floral visits for each minute of survey time that an individual cactus had at least one open flower. Sample sizes for each category are shown above each bar; results of two-sample t-tests appear above each pair of bars (ns = non-significant). For each type of bee, two-sample t-tests compare rates of visitation between cacti controlled by the two ant species.

Figure 3

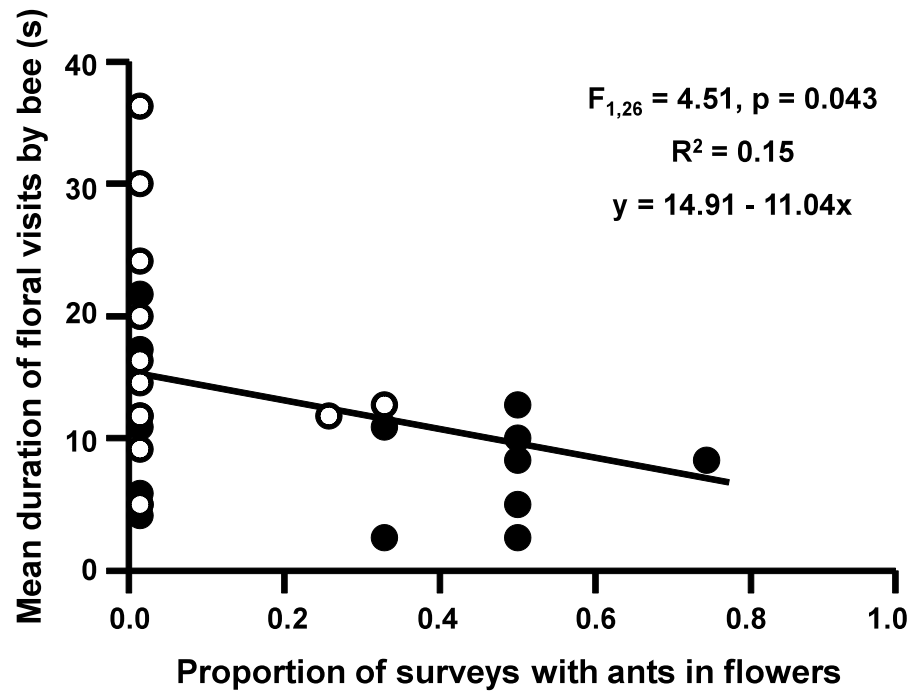


Figure 3. Simple linear regression of the mean duration of floral visits by bees versus the proportion of survey visits in which we observed ants in cactus flowers. Each data point represents bee and ant activity on an individual cactus. Open circles show cacti controlled by *Crematogaster californica*; closed symbols show cacti controlled by *Linepithema humile*. Cacti not visited by bees are omitted from this analysis.

Figure 4

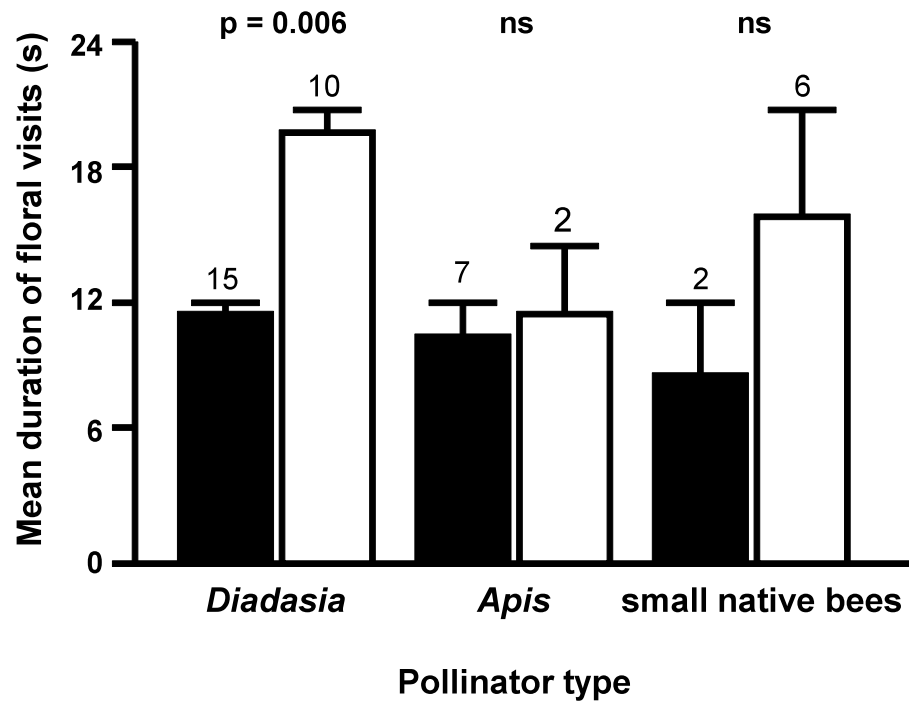


Figure 4. The mean (\pm SE) duration of floral visits by *Diadasia*, *Apis mellifera*, and small native bees. Open bars show cacti controlled by *Crematogaster californica*; closed bars show cacti controlled by *Linepithema humile*. Each datum is the mean duration of the floral visits for one type of bee on an individual cactus. Sample sizes for each category are shown above each bar; results of two-sample t-tests appear above each pair of bars (ns = non-significant). For each type of bee, two-sample t-tests compare rates of visitation between cacti controlled by the two ant species.

Figure 5

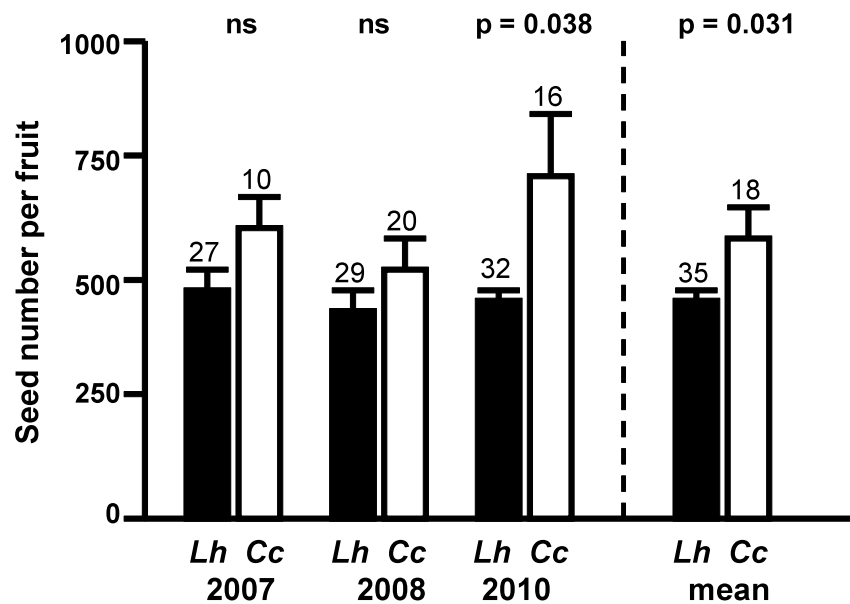


Figure 5. The mean (\pm SE) number of seeds per fruit when controlling for number of fruit per cactus. Open bars show cacti controlled by *Crematogaster californica*; closed bars show cacti controlled by *Linepithema humile*. Number of seeds per fruit was determined by weighing 100 seeds, obtaining a weight per seed and using the formula (total weight of all seeds/ weight per seed) to obtain a total number of seeds per fruit. Mean category is an average of seed number per fruit across all years of data available. Sample sizes for each category are shown above the bar; results of two-sample t-tests appear above each pair of bars (ns = non-significant).

Figure 6

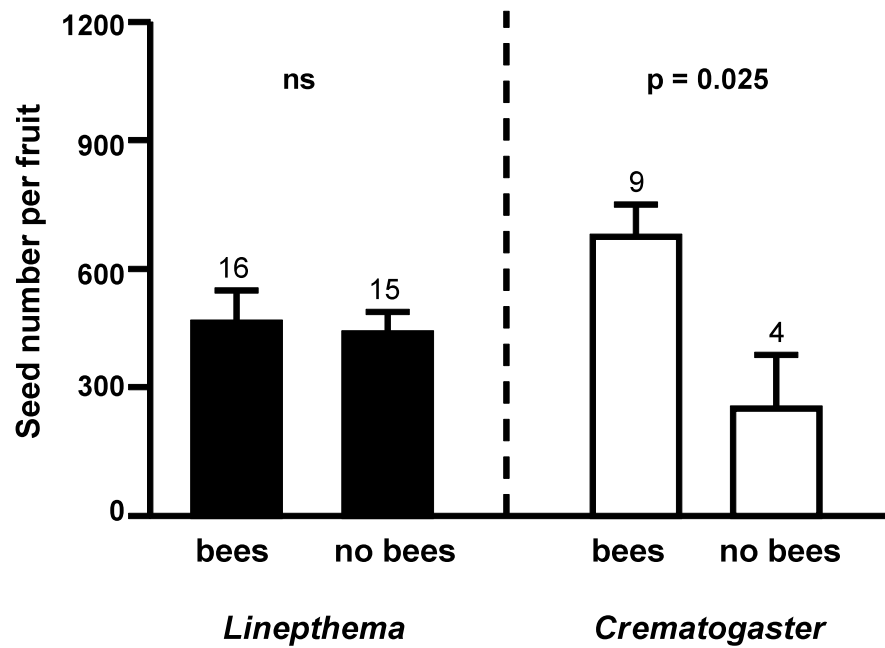


Figure 6. The mean (\pm SE) number of seeds per fruit of cactus of which we have pollinator visitation data. Open bars show cacti controlled by *Crematogaster californica*; closed bars show cacti controlled by *Linepithema humile*. Each data point represents one cactus as categorized as either yes or no for bee visitation over the 2010 floral season. Sample sizes for each category are shown above each bar; results of two-sample t-tests appear above each pair of bars (ns = non-significant). For each type of cactus, two-sample t-tests compare seed number per fruit between cacti either visited by bees or not.

Table 1. Mean (\pm SE) physical characteristics of focal cacti in the 2010 pollinator survey. Cacti were controlled by either *Linepithema humile* (n = 32) or *Crematogaster californica* (n = 16).

	<i>L. humile</i>	<i>C. californica</i>	t-test*
volume (cm ³)	2613.3 \pm 282.1	2852.7 \pm 382.5	ns
number of floral buds	23.6 \pm 2.0	28.7 \pm 4.9	ns
number of flowers	18.9 \pm 1.8	20.2 \pm 3.8	ns
blooming period (days)	40.1 \pm 1.6	40.1 \pm 3.4	ns
number of fruit	14.8 \pm 1.1	16.8 \pm 3.4	ns

* Cacti controlled by each ant species were compared with respect to each characteristic. ns = not significant comparisons from two-sample t-tests.

REFERENCES

- Baker, H. G. 1972. Seed weight in relation to environmental conditions in California. *Ecology* 53 (6): 997-1010.
- Beattie, A. J. 1985. The evolutionary ecology of ant-plant mutualisms, Cambridge University Press.
- Bowers, J.E. and E. A. Pierson. 2001. Implications of seed size for seedling survival in *Carnegiea gigantea* and *Ferocactus wislizeni* (Cactaceae). *The Southwestern Naturalist* 46(3): 272-281.
- Bronstein, J.L. 1994. Conditional outcomes in mutualistic interactions. *TRENDS in Ecology and Evolution* Vol. 9, No.214: 214-217.
- Bronstein, J. L. 2001. The exploitation of mutualisms. *Ecology Letters* 4: 277-287.
- Glenn, S. & D.A. Holway. 2008. Consumption of introduced prey by native predators: Argentine ants and pit-building ant lions. *Biological Invasions* 10: 273-280
- Holway, D.A. 1995. Distribution of the Argentine ant (*Linepithema humile*) in northern California. *Conservation Biology* 9: 1634-1637.
- Holway, D.A., L. Lach, A.V. Suarez, N.D. Tsutsui and T.J. Case. 2002. The causes and consequences of ant invasions. *Annual Review of Ecology & Systematics* 33:181-233.
- Holway, D.A., 2005. Edge effects of an invasive species across a natural ecological boundary. *Biological Conservation* 121: 561-567.
- Holway D.A. and Andrew Suarez. 2006. Homogenization of ant communities in Mediterranean California: The effects of urbanization and invasion. *Biological Conservation* 127:319-326.
- Ingram, S. 2008. Cacti, agaves, and yuccas of California and Nevada. Cachuma press 2008.

- Lach, L. 2003. Invasive ants: unwanted partners in ant-plant interactions? *Annals of the Missouri Botanical Garden*, Vol. 90 (1): 91-108.
- Lach, L. 2007. A mutualism with a native membracid facilitates pollinator displacement by argentine ants. *Ecology* 88 (8): 1994-2004.
- Lach, L. 2008. Argentine ants displace floral arthropods in a biodiversity hotspot. *Diversity and Distributions* 14 (2): 281–290
- McGrady-Steed, J., P. M. Harris, and P.J. Morin. 1997. Biodiversity regulates ecosystem predictability. *Nature* 390 (13): 162-164.
- McIntosh, M.E. 2002. Flowering phenology and reproductive output in two sister species of *Ferocactus* (Cactaceae). *Plant Ecology* 159: 1-13.
- Menke, S. and D.A. Holway. 2006. Abiotic factors control invasion by Argentine ants at the community scale. *Journal of Animal Ecology* 75 (2): 368-376.
- Menke, S., R.N. Fisher, W. Jetz, and D.A. Holway. 2007. Biotic and abiotic controls of Argentine ant invasion success at local and landscape scales. *Ecology* 88(12): 3164-73.
- Miller, T. E. X. 2007. Does having multiple partners weaken the benefits of facultative mutualism? A test with cacti and cactus-tending ants. *Oikos* 116: 500-512.
- Morris, W.F., W.G.Wilson, J.L.Bronstein and J.H.Ness. 2005. Environmental forcing ant the competitive dynamics of a guild of cactus-tending ant mutualists. *Ecology* 86 (12): 3160-3199.
- Myers, N. and A.H. Knoll. 2001. The biotic crisis and the future of evolution. *Proceedings of the National Academy of Sciences* 98 (10): 5389-5392.
- Naeem, S. 1998. Species redundancy and ecosystem reliability. *Conservation Biology* 12 (1): 39-45.

- Ness, J. H. and J. Bronstein. 2004. The effects of invasive ants on prospective ant mutualists. *Biological Invasions* 6: 445-461.
- Ness, J. H. 2006. A mutualism's indirect costs: the most aggressive plant bodyguards also deter pollinators. *OIKOS* 113: 506-514.
- Ness, J., W.F. Morris, and J.L. Bronstein. 2006. Integrating quality and quantity of mutualistic service to contrast ant species protecting *Ferocactus wislizeni*. *Ecology*, 87(4): 912-921.
- Schilman, P. E., J.R.B. Lighton, and D.A. Holway. 2005. Respiratory and cuticular water loss in insects with continuous gas exchange: comparison across five ant species. *Journal of Insect Physiology* 51 (12): 1295-1305.
- Suarez, A.V., D.T. Bolger, and T.J. Case. 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. *Ecology* 79:2041-2056
- Traveset, A. and D. Richardson. 2006. Biological invasions as disruptors of plant reproductive mutualisms. *TRENDS in Ecology and Evolution* Vol. 21, No.4: 208-216.
- Stanton, M.L., Palmer, T.M., Young, T.P., Evans, A. and Turner, M.L. 1999. Sterilization and canopy modification of a swollen thorn acacia tree by a plant-ant. *Nature* 401: 578-581.
- Ward, P.S. 1987 Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the Lower Sacramento Valley and its effects on the indigenous ant fauna. *Hilgardia* 55, 1-16.
- Winfrey, R., N.M. Williams, J. Dushoff, C. Kremen. 2007. Native bees provide insurance against ongoing honey bee losses. *Ecology Letters* 10: 1105-1113.
- Palmer, T., M., M.L. Stanton, T.P. Young, J. R. Goheen, R.M. Pringle, R. Karban. 2008. Breakdown of an ant-plant mutualism follows the loss of large herbivores from an African savanna. *Science* 319:192-194.
- Zee, J. and D. Holway. 2006. Nest raiding by the invasive Argentine ant on colonies of the harvester ant, *Pogonomyrmex subnitidus*. *Insectes Sociaux* 53 (2): 161-167.