

Enough is enough: the effects of symbiotic ant abundance on herbivory, growth, and reproduction in an African acacia

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Abstract. Understanding how cooperative interactions evolve and persist remains a central challenge in biology. Many mutualisms are thought to be maintained by “partner fidelity feedback,” in which each partner bases their investment on the benefits they receive. Yet, we know little about how benefits change as mutualists vary their investment, which is critical to understanding the balance between mutualism and antagonism in any given partnership. Using an obligate ant–plant mutualism, we manipulated the density of symbiotic acacia ants (*Crematogaster mimosae*) and examined how the costs and benefits to *Acacia drepanolobium* trees scaled with ant abundance. Benefits of ants to plants saturated with increasing ant abundance for protection from branch browsing by elephants and attack by branch galling midges, while varying linearly for protection from cerambycid beetles. In addition, the risk of catastrophic whole-tree herbivory by elephants was highest for trees with very low ant abundance. However, there was no relationship between ant abundance and herbivory by leaf-feeding invertebrates, nor by vertebrate browsers such as giraffe, steinbuck, and Grant’s gazelle. Ant abundance did not significantly influence rates of branch growth on acacias, but there was a significant negative relationship between ant abundance and the number of fruits produced by host plants, suggesting that maintaining high-density ant colonies is costly. Because benefits to plants largely saturated with increasing colony size, while costs to plant reproduction increased, we suggest that ant colonies may achieve abundances that are higher than optimal for host plants. Our results highlight the conflicts of interest inherent in many mutualisms, and demonstrate the value of examining the shape of curves relating costs and benefits within these globally important interactions.

Key words: *Acacia drepanolobium*; ant–plant relationships; *Crematogaster mimosae*; defense investment; herbivory; Kenya; mutualism; partner fidelity feedback; plant defense.

INTRODUCTION

Mutualisms are among the most widespread and economically important species interactions on earth (Bronstein 1994, Stachowicz 2001, Sachs and Simms 2006, Bronstein 2009). Yet, they have long been viewed as an evolutionary paradox: how does cooperation persist when natural selection should favor individuals that reap maximum benefit for minimum cost (Darwin 1859)? One condition that should favor the stability of mutualisms is when increased investment yields a higher net return (i.e., “partner fidelity feedback”; Bull and Rice 1991, Doebeli and Knowlton 1998, Sachs et al. 2004). An increase on return with increased investment often occurs when symbionts are transferred vertically from host to progeny (e.g., *Wolbachia* and insects, plants and endophytes). In contrast, for horizontally transmitted symbioses (e.g., plant–mycorrhizal or coral–dinoflagellate mutualisms), neither party gains from the

reproduction of its mutualist partner, thus the potential for conflicts of interest increase. Establishing the range of conditions over which interactions remain mutualistic, and when they tip to antagonism, requires evaluating how the costs and benefits scale with investment.

Increased investment by mutualists can increase partner abundance, and variation in partner abundance is expected to be a major axis along which the payoffs of mutualism depend (Bronstein 1998). Despite this, relatively few empirical studies have investigated the functional form of the relationship between partner abundance and the costs and benefits of mutualism (e.g., Duarte Rocha and Godoy Bergallo 1992, Johnson et al. 1997, Gange and Ayres 1999, Holland et al. 2002, Morris et al. 2010, Vannette and Hunter 2011). Obligate ant–plant protection relationships, in which ants protect plants from enemies in exchange for living space and/or food, offer ideal systems to examine the cost/benefit relationship (reviewed in Bronstein 1998, Heil and McKey 2003). Within obligate ant–plant interactions, ant plants (“myrmecophytes”) provide a number of benefits to ants, including nest space and food rewards. In return, ants may provide protection from herbivory

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and/or encroaching vegetation, as well as nutrient enrichment to the plant (reviewed in Davidson and McKey 1993, Heil and McKey 2003). Often, larger plants support more ants (Duarte Rocha and Godoy Bergallo 1992, Frederickson and Gordon 2009); an increased investment by plants in ants leads to larger ant colonies (Heil et al. 2001, Itino et al. 2001); and larger ant colonies provide greater protective benefits (Gaume et al. 1998, Heil et al. 2001, Goheen and Palmer 2010). What is less well understood is how the costs and benefits of ant associates scale with their abundance on host plants (Frederickson and Gordon 2009). For plants that feed ants, the cost of supporting ant colonies likely increases with increasing ant density because each additional ant proportionally increases the metabolic demand on the host plant (Fonseca 1993). However, the protective benefits of ants may be a saturating function if adding ants to an already large colony yields little or no increased protection (Duarte Rocha and Godoy Bergallo 1992, Fonseca 1993, but see Frederickson and Gordon 2009). From the ant colony's perspective, however, selection may favor colonies larger than those optimal for plants (Heil and McKey 2003). For example, larger colonies are better able to defend nest sites from usurpation by neighboring colonies (Holldobler and Wilson 1990, Palmer 2004). As a consequence, there may be destabilizing conflicts of interest between plants and ants in "optimal" colony size.

Here, we evaluate how the demographic costs and protective benefits of plant-ants scale with colony size of *Crematogaster mimosae*, a common ant associate of *Acacia drepanolobium*, which is widespread throughout East Africa (Hocking 1970). Within this ant-plant system, *A. drepanolobium* trees provide both nest space ("swollen thorn" domatia) and carbohydrate-rich extrafloral nectar for ants, and ants provide protection from both invertebrate and vertebrate herbivores (Young et al. 1997, Palmer and Brody 2007). The system is well suited for our study for a variety of reasons: (1) *Crematogaster mimosae* actively defends its hosts from a variety of invertebrate and vertebrate herbivores; (2) the protective benefits of *Acacia* ants appear to depend on ant activity levels and their aggressiveness (Palmer and Brody 2007, Goheen and Palmer 2010); (3) there may be conflicts of interest between these ants and their plant partners as maintaining ant symbionts is costly for acacias (Stanton and Palmer 2011); and (4) there is likely strong selection on ants to attain large colony sizes, because colony size is directly linked to the ability of *C. mimosae* to defend its trees from inter- and intraspecific takeover by neighboring colonies (Palmer 2004). To increase their colony size, *C. mimosae* constructs "carton" from plant and waste material to form multiple "floors" or levels within domatia, thereby doubling the number of workers that can reside within each swollen thorn (Palmer 2004). In addition, *C. mimosae* colonies tend to scale insects on host plants, allowing them to access

plant carbohydrates through the consumption of both extrafloral nectar and scale exudates.

Although larger colony size provides clear benefits to *C. mimosae* (Palmer 2003, 2004, Palmer et al. 2008), it is unclear if the benefits of hosting more defenders outweighs the cost to the host tree. To quantify how ant abundance affects herbivory, growth, reproduction, and survival of *A. drepanolobium*, we experimentally manipulated *C. mimosae* colony size and examined the functional form of the relationship between ant density and (1) levels of damage to trees by different types of herbivores and (2) host plant growth, reproduction, and survival over the course of a one-year period. We tested whether herbivore damage was a linear or saturating function of ant abundance on host plants. If benefits saturate while costs increase with increasing colony size we might expect a quadratic (unimodal) relationship between ant abundance and plant performance; thus we then tested whether growth and reproduction of host plants was best fit by a linear or quadratic model, and whether plant mortality varied as a function of ant density. To better interpret our data on the effectiveness of ant defense against different herbivores, we also conducted scans of patrolling workers on different parts of host plants across a range of ant abundances.

METHODS

We conducted our study at the Mpala Research Centre, located within Laikipia district of the central highlands of Kenya (0°17' N, 37°52' E; 1800 m elevation). In our study area, *A. drepanolobium* accounts for >97% of canopy cover, forming a near-monoculture in the overstory (Young et al. 1997). *Acacia drepanolobium* is a small tree, defended by stipular spines and symbiotic ants (Milewski et al. 1991, Young et al. 1997, Palmer and Brody 2007). On each host plant, ants are housed within swollen thorn domatia, bulbous structures up to 5 cm in diameter located at the base of the spine. Ants feed in part from extrafloral nectaries, located at the base of the rachis of leaves. Virtually all trees >1 m tall have a single resident ant colony, although a colony may occupy multiple trees. In this study, we focus on host plants occupied by *Crematogaster mimosae*, a specialist on *A. drepanolobium*, which occupies ~50% of host trees at our study site and depends entirely on the interiors of swollen thorns for nesting space. The remaining *A. drepanolobium* are occupied by three other ant species, *C. nigriceps*, *C. sjostedti*, and *Tetraponera penzigi* (Hocking 1970).

We randomly chose 80 *A. drepanolobium* host plants along a 300-m transect, subject to the condition that each was occupied by an active *C. mimosae* colony. Because a single *C. mimosae* colony can occupy multiple trees (Palmer 2004), we selected trees that were separated by at least 10 m to ensure that experimental trees were occupied by different colonies. Trees were approximately matched for height (1.6–2.1 m), canopy volume, swollen thorn number, and ant activity levels.

Ant activity levels were assessed by sharply disturbing an arbitrarily chosen swollen thorn on both an east- and west-facing branch at chest height, and recording the number of ants swarming (Palmer et al. 2008). After experimental trees were selected, we assigned each group of four consecutive trees along the transect to one of four treatments: (1) control, (2) approximately one-third ant removal, (3) approximately two-thirds ant removal, and (4) full ant removal. *Crematogaster mimosae* evacuates host plants (including removing its brood along with winged reproductive males and females) when they detect smoke from bush fires. Taking advantage of this behavior, we removed ant colonies by inundating the host plant with smoke generated by burning dry grass in a bucket underneath the tree. Prior to the application of smoke, one of us picked an arbitrary point ~50 cm above the ground on the shaded side of tree to observe (when ants swarm off trees in response to smoke, they do so on the side of the tree that is in shade). As smoke was applied, we counted ants, in multiples of 50 as they crossed the 50-cm aboveground, imaginary horizontal line. The count provided a rough estimate of the total number of workers occupying the tree. When host plants were close to fully evacuated (<50 workers appearing on branches after vigorously shaking the canopy), we allowed either no ants, approximately one-third of ants, approximately two-thirds of ants, or the entire colony to recolonize the tree, and applied duct tape covered by a Tanglefoot (Contech Enterprises, Grand Rapids, Michigan, USA) sticky barrier at the tree's base to prevent further colonization. Duct tape and Tanglefoot were applied to all control trees as well. After seven days, we revisited the trees to assess levels of ant defensive activity, which we used as a surrogate for ant density. To assess ant activity, we arbitrarily chose two branches at a height of 1.5–2.0 m, one on the south side of the canopy and one on the north. One of us, wearing a leather glove, grasped the branch tip and raked the first 15 cm of the branch three times in rapid succession. We recorded the number of ants swarming onto the leather glove during a 30-s period for both branches. We used the mean of these two numbers as an index of overall ant abundance for each tree (Palmer and Brody 2007).

To examine the costs of hosting ant colonies of different sizes, we measured branch growth and production of swollen thorns. We arbitrarily chose two terminal branches at a height of 1.5–2.0 m, one on the east side of the canopy and one on the west side. Each branch was marked at a distance of 15 cm from the apex of the branch with a colored zip-tie, and the total length of the branch was measured, as well as the number of swollen thorns present. We then resurveyed these branches at the end of the experiment.

We maintained treatments for a period of one year. Trees were visited at bimonthly intervals to maintain Tanglefoot barriers. At 4, 8, and 12 months, we conducted ant activity surveys to confirm that colonies

remained at treatment levels; ant abundance did not decrease or increase significantly over the course of the 12-month experiment (comparison of slopes of time vs. ant abundance to hypothesized value of 0; Student's *t* test, $t = -0.23$, $P = 0.82$).

After 12 months, we resurveyed trees and calculated the average ant abundance on each tree over the four censuses. We measured growth and counted swollen thorns on each of the marked branches. We also surveyed each tree for reproduction, for damage by different classes of herbivores, and for survival. We recorded presence or absence of fruits on each tree, and counted total fruits if trees were fruiting. We also scored each tree for the presence and number of scars or sap-exuding wounds inflicted by stem-boring cerambycid beetles (Stanton and Palmer 2011), and the total number of branch galls (sites of attack by galling midges) present on all branches. To assess levels of damage by vertebrate browsers, we examined all branches on each tree for characteristic signs of browsing, including bite marks, nipped branch tips, and bark stripping. Browsing by elephants (large broken branches, extensive bark stripping, and obliterated trees) was distinguished from damage by other vertebrate browsers (e.g., giraffe, eland, Grant's gazelle, and steinbuck). To assess levels of invertebrate damage to foliage (largely aerially colonizing invertebrates, such as leaf-feeding beetles and grasshoppers) we arbitrarily removed five fully developed leaves from branches occurring at a height of 1–2 m around the entire circumference of focal trees. Leaves were selected from within the first 10 cm of new growth on branch tips. We then visually estimated the percentage of leaflets bearing signs of insect damage (including both missing and chewed leaflets), assigning each leaf to one of four damage categories (1, 0–25%; 2, 26–50%; 3, 51–75%; 4, 76–100%). We used the mean value of each damage class in analyses.

To evaluate how changes in abundance influenced colony behavior with respect to the number of workers patrolling different plant parts, we established another transect of plants with colony sizes manipulated, and conducted scans of worker activity on these plants. We surveyed the number of patrolling workers on three different tree regions that are typical sites of attack by different invertebrate herbivores: terminal branches with diameters <3 cm (typical sites of galling midge attack, hereafter "branches"), larger branches or stems >3 cm diameter (typical sites of cerambycid beetle attack, hereafter "stems"), and mature leaves (typical sites of leaf feeding invertebrate herbivores). To establish this second set of density manipulations, we located 45 *A. drepanolobium* along a 1000-m transect, each between 1.6 and 2.1 m tall and occupied by *C. mimosae*. We assigned consecutive trees to one of three treatments: (1) 33% of swollen thorns removed, (2) 66% of swollen thorns removed, and (3) controls, with no swollen thorns removed. We counted swollen thorn domatia on each host plant and removed the corresponding

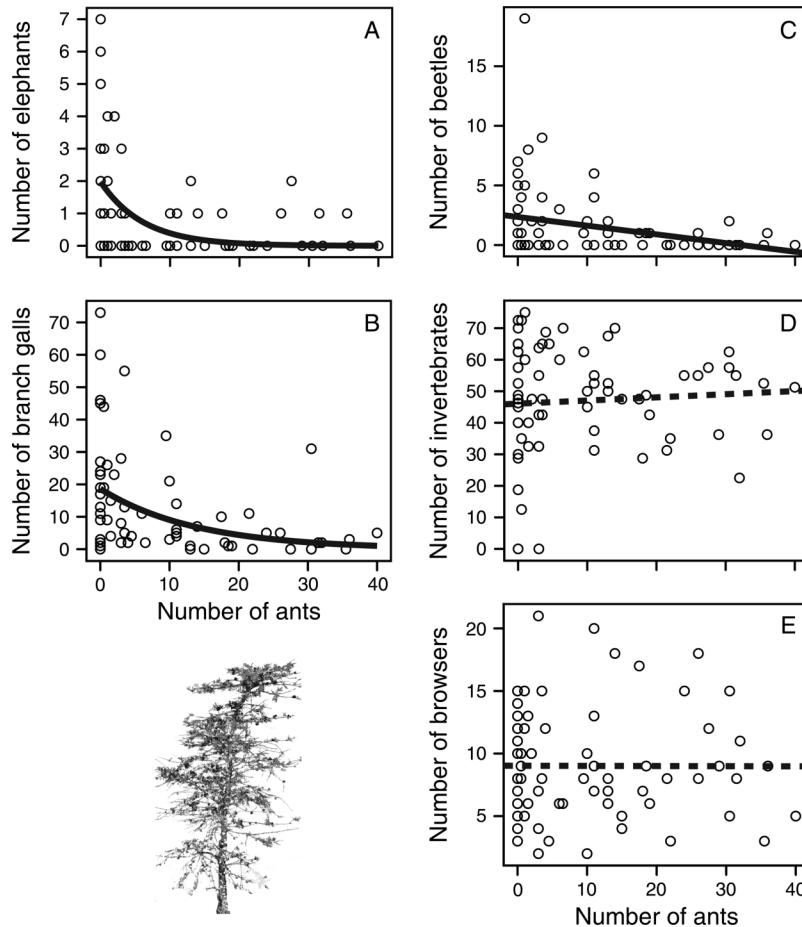


FIG. 1. The number of ants (*Crematogaster mimosae*) swarming onto thorn tips of *Acacia drepanolobium* during 30-s intervals vs. herbivore damage by different types of herbivores at the Mpala Research Centre, Kenya: (A) number of branches browsed by elephants, (B) number of galls on host plants, (C) number of sites of cerambycid beetle damage, (D) percentage of leaflets chewed per five leaves, and (E) number of branch tips damaged by non-elephant vertebrate browsers. Best-fitting regression lines are shown for each data set; solid lines indicate slope parameters that differ significantly from zero.

percentage of swollen thorns with pruning shears, taking care only to clip the lignified portion of each domatia. We then revisited plants after 12 months and recorded the number of workers patrolling different plant parts. Three observers approached each plant from downwind, taking care not to disturb the resident colony. Each observer then chose an arbitrary section of the host plant canopy at chest height (1.5 m) and counted the number of workers patrolling on a 20-cm length of (1) a terminal branch (diameter <3 cm), (2) a larger plant stem (>3 cm diameter), and (3) fully expanded leaves along a terminal branch.

Statistical analyses

First, we asked if higher levels of ant abundance on host plants resulted in continuous gains in anti-herbivore protection, or if the benefits of increasingly large colonies saturated. Our initial ant removal method (via smoke inundation) created a continuous distribution of ant abundance on experimental plants. We

analyzed herbivore damage, growth rate, and the number of fruits produced on trees as response variables, regressed against average ant abundance on each plant over the four censuses. Fruiting data were square-root transformed to satisfy normality requirements. We compared the fit of linear vs. negative exponential models using AIC_c (Akaike's Information Criterion for small samples). We analyzed the relationship between ant abundance and tree survival over the one-year period using logistic regression. Last, we evaluated differences in the number of workers patrolling different plant parts on host plants with different colony sizes using nested ANOVA; means comparisons were conducted using Tukey-Kramer HSD tests. All statistical analyses were performed in JMP 10 (SAS Institute, Cary, North Carolina, USA).

RESULTS

The efficacy of ants in defending plants varied for different types of herbivory (Fig. 1). For elephant

TABLE 1. Best-fit regression models for effects of ant (*Crematogaster mimosae*) density on different forms of herbivory on *Acacia drepanolobium* at the Mpala Research Centre, Kenya.

| Herbivory type | Best-fit model | Estimated coefficients | | | |
|-------------------|-----------------------|------------------------|------|----------|------|
| | | <i>a</i> | SE | <i>b</i> | SE |
| Elephant | negative exponential† | 1.96 | 0.25 | −0.14 | 0.06 |
| Galling midge | negative exponential† | 20.07 | 2.88 | −0.08 | 0.03 |
| Cerambycid beetle | linear† | 3.01 | 0.52 | −0.09 | 0.03 |
| Folivorous insect | linear | 51.44 | 2.23 | −0.12 | 0.14 |
| Browsing mammal | linear | 9.02 | 0.67 | −0.001 | 0.04 |

Notes: Best-fit models were selected using AIC_c from linear vs. negative exponential regression analyses of the effects of ants on different forms of herbivory. All analyses were performed in JMP (version 10).

† The 95% confidence intervals around slope parameter do not overlap zero.

damage and attack by galling midges, a negative exponential model provided the best fit to the data ($\Delta AIC_c = 5.13$ and 2.84 for elephants and galling midges, respectively), whereas a linear model provided a marginally better fit for cerambycid damage ($\Delta AIC_c = 0.37$; Fig. 1, Table 1). Damage by browsers other than elephants (e.g., giraffe and steinbuck) and folivorous insects was uncorrelated with ant density (Fig. 1, Table 1). By the end of the second week of our experiment, a herd of elephants had completely destroyed four of the “total ant removal” host plants, and a fifth plant that had relatively low densities of resident *C. mimosae* (“two-thirds colony removal” tree); in contrast, none of the control trees were destroyed. Logistic regression of these data revealed that the probability of elephant-induced mortality was significantly higher for plants with low ant abundances ($\chi^2 = 5.70$, 1 df, $P < 0.02$).

Ant abundance did not significantly affect rates of branch growth or swollen thorn production (Table 2). However, the number of fruits produced by trees was negatively related to ant abundance at the experiment’s end (Fig. 2, Table 2).

More workers patrolled branches on trees supporting more populous colonies (Fig. 3; $F_{2,6} = 14.2$, $P < 0.0001$), and the number of patrolling workers differed among parts of host plants (Fig. 3; $F_{2,6} = 19.8$, $P < 0.0001$). Patroller numbers on fully expanded leaves was low overall, and did not vary significantly on host plants with different ant abundances (Fig. 3; Tukey’s HSD tests). In contrast, patrolling worker numbers increased and then saturated with increasing colony size on

terminal branches, and increased with increasing colony size on larger (>3 cm diameter) stems (Fig. 3; Tukey’s HSD tests).

DISCUSSION

Do the protective benefits of hosting defensive ant symbionts increase linearly or saturate with increasing ant abundance? Our results show that the answer to this question varies depending on the type of herbivory considered. Herbivory by *A. drepanolobium*’s most damaging consumer, the African elephant, showed a rapidly saturating relationship with colony size, with intermediate-sized colonies providing similar levels of protection as larger colonies. Elephants, which impose strong and potentially catastrophic damage to host plants, typically avoid *A. drepanolobium* with intact colonies (Goheen and Palmer 2010). Our results suggest that even at lower abundance, *C. mimosae* provides strong defense against elephants (see Plate 1). When disturbed, *C. mimosae* workers produce a potent alarm pheromone (Wood et al. 2002), and our field observations suggest that elephants use these olfactory cues (Fig. 4) in their feeding decisions on individual plants (J. R. Goheen and T. M. Palmer, *personal observation*).

We also found a saturating relationship between ant abundance and host plant attack by galling midges, again suggesting that colonies at intermediate sizes provided similar levels of protection from these plant parasites. Because galling midges typically attack growing terminal branches where *C. mimosae* workers concentrate much of their activity, colonies of interme-

TABLE 2. Best-fit regression models for effects of ant density on *A. drepanolobium* twig growth, swollen thorn production, and fruiting.

| Plant trait | Best-fit model | Estimated coefficients | | | |
|--------------------------|----------------|------------------------|-------|----------|------|
| | | <i>a</i> | SE | <i>b</i> | SE |
| Twig growth | linear | 63.03 | 10.02 | −1.04 | 0.68 |
| Swollen thorn production | linear | 3.39 | 0.70 | 0.02 | 0.05 |
| Number of fruits | linear† | 4.64 | 0.52 | −0.07 | 0.03 |

Notes: Best-fit models were selected using AIC_c from linear vs. quadratic regression analyses of the effects of ants on plant growth and reproduction. All analyses were performed in JMP (version 10).

† The 95% confidence intervals around the slope parameter do not overlap zero.

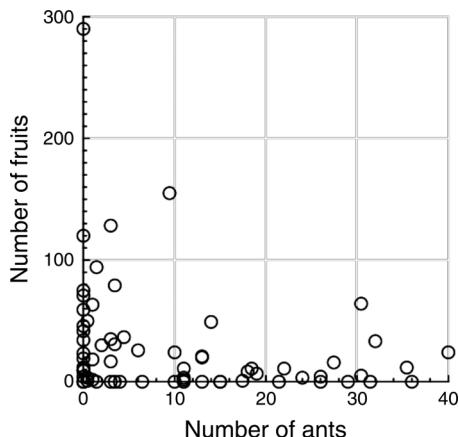


FIG. 2. The number of fruits produced by *Acacia drepanolobium* host plants that differed in resident ant colony density.

diate abundance appeared to be similarly effective as high abundance colonies against these plant enemies. Our scans of numbers of patrolling workers on host plants with different colony sizes supported this interpretation; host plants on which colonies had been reduced to low size (two-thirds of total domatia removed) had fewer workers patrolling terminal branches, while intermediate-sized colonies (one-third of total domatia removed) did not differ significantly from control (nonreduced) colonies in the number of workers patrolling branches.

For cerambycid beetle attack, the linear and negative exponential models provided similar fits ($\Delta AIC_c = 0.37$), and beetle attack declined with increasing ant abundance. Adult cerambycids chew bark scars on *Acacia drepanolobium* stems where they deposit eggs, which grow into larvae that tunnel through stem wood as they mature; attack by these beetles is correlated with strong reductions in host plant growth and increases in plant mortality over time (Palmer et al. 2008). Because cerambycids attack all woody surfaces of trees, including the trunk and branches, colonies with lower patroller densities may be less effective at discovering these enemies while they are ovipositing, thus leading to greater rates of plant attack. Again, our scans of patrolling workers on sites typical of cerambycid attack (stems >3 cm diameter) supported this interpretation; the number of patrolling workers found on larger diameter branches increased with increasing colony size.

In contrast, *C. mimosae* were not effective in deterring herbivory by leaf-feeding invertebrates and non-elephant vertebrate browsers. *C. mimosae* workers did not typically patrol the surfaces of fully developed leaves; consequently, damage by small invertebrate herbivores was unaffected by ant numbers. Likewise, observations and analysis of video of foraging giraffes (a major herbivore that we observe feeding on *A. drepanolobium* of this size class; T. Palmer, *personal observation*) indicate that these browsers are little deterred by *Acacia*

ants, using their prehensile tongues to wipe away attacking ants from their faces and mouthparts. Our observations are consistent with results from Madden and Young (1992) who found that feeding bout duration by adult giraffes did not vary between *A. drepanolobium* with high vs. low ant densities. In contrast, attack by *Crematogaster nigriceps* (an equally aggressively defending congener of *C. mimosae*; Palmer and Brody 2007) deterred domestic goats from returning to feed at *A. drepanolobium* trees (Stapley 1998), but unlike wild browsing herbivores found at our study site (steinbuck, Grant's gazelle, eland), goats do not typically feed on *A. drepanolobium* and therefore may be more susceptible to ant defense.

Do plants pay a cost for greater defense? Although ants were effective at defending plants from attack by both elephants and cerambycid beetles, supporting larger ant colonies appeared to impose significant demographic costs to host plants. Although we found no differences in branch growth rates or swollen thorn production among trees supporting different ant densities, there was a significant negative relationship between ant abundance and the number of fruits produced by acacias. *Crematogaster mimosae* workers feed on extrafloral nectar as well as tend phloem-feeding insects within swollen thorns. Thus, the metabolic costs of supporting colonies are likely to scale with colony size. Our results suggest that these costs are sufficiently high for larger colonies to reduce host plant reproduction, even over a relatively short time (one year). Indeed, results of a 4.5-year ant removal experiment demonstrated that occupation by *C. mimosae* was associated with significantly reduced host plant reproduction relative to ant-removal trees, despite ant-removal trees

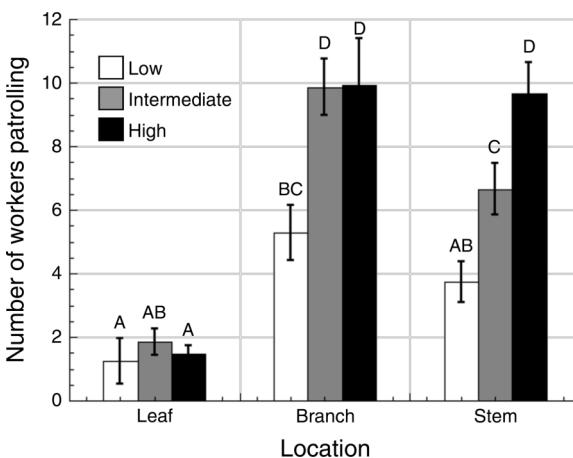


FIG. 3. The number of workers (mean \pm SE) patrolling on plant parts of *Acacia drepanolobium* that differed in colony density during 30-s scans. "Low" ant density refers to host plants where two-thirds of domatia were removed, "intermediate" refers to plants where one-third of domatia were removed, and "high" refers to plants where no domatia were removed. Uppercase letters show means that differ significantly in Tukey-Kramer HSD tests ($P < 0.05$).



FIG. 4. An African elephant (*Loxodonta africana*) tests the air above an *A. drepanolobium* before feeding on the tree's foliage. Photo credit: K. Rudolph.

suffering much higher rates of herbivory (Stanton and Palmer 2011). Congruent with this pattern, defensive ant symbionts other than *C. mimosae* may impose costs to plant reproduction by deterring pollinators (Ness 2006) or sterilizing host plants by removing floral buds or flowers (Yu and Pierce 1998, Stanton et al. 1999, Gaume et al. 2005). Taken together, these results point to a potential trade-off between biotic defense and reproduction for *A. drepanolobium*, as has been suggested for structural defense (stipular spines) in this species (Goheen et al. 2007).

Although trees experienced high reproductive costs in supporting ants, our experiment also serendipitously revealed a strong but more sporadic benefit of ant symbionts, protection from catastrophic herbivory (predation) by elephants. Elephant herbivory on *A. drepanolobium* is rare (Goheen and Palmer 2010) but can be catastrophic. So, while costs of providing extrafloral nectar and domatia for ants continually accrue, the major benefit of elephant protection may be realized across much longer time scales (Stanton and Palmer 2011). *Acacia drepanolobium* often live >100 years. Thus, the high reproductive costs of supporting ants may be a metabolically expensive "insurance policy" to guard against infrequent but devastating herbivory. Our results reinforce previous work suggesting that elephant herbivory is a major selective force driving the evolution and persistence of this ant-plant association (Palmer et al. 2008, Goheen and Palmer 2010).

Are typical colony sizes of *C. mimosae* optimal for their hosts? Our data show that *C. mimosae* colonies at experimentally reduced abundances conferred similar

levels of protection as high abundance colonies from two major herbivores, elephants and galling midges, while imposing lower costs in terms of plant reproduction, suggesting a potential conflict of interest between *A. drepanolobium* and its most common ant associate. Although the production of domatia and extrafloral nectaries by *A. drepanolobium* is phenotypically plastic (Palmer et al. 2008), and thus might provide plants a means of regulating symbiont populations (e.g., Izzo and Vasconcelos 2002), *C. mimosae* may be able to circumvent such controls by building carton within swollen thorns to increase habitable nest space, and tending scale insects to directly access plant carbohydrates. As a result, this ant species is able to achieve very high densities on individual plants in the field (up to 25 000 workers on a 2.0-m tree; T. M. Palmer, unpublished data). Large colonies are better able to defend their trees from hostile takeover by neighboring colonies (Palmer 2004). Although our data suggest that *C. mimosae* densities may exceed optimal levels for plants, two important caveats should be noted. First, the abundance of *C. mimosae* has consequences not just for herbivore protection, but within a broader community context; plants occupied by large colonies of this aggressive ant species are at lower risk of takeover by the competitively dominant *C. sjostedti*, a large colony-size congener, which does not protect plants from herbivores and facilitates beetle attack of its host (Palmer 2004, Stanton and Palmer 2011). Thus, maintaining high-density *C. mimosae* colonies may generate partner fidelity feedback, allowing plants more persistent relationships with this strongly protecting ant



PLATE 1. A group of African elephants (*Loxodonta africana*) feeds on forbs and grasses within *Acacia drepanolobium* savanna. The elephants typically avoid feeding on the acacias, as these trees are vigorously defended by large colonies of aggressive ants. Photo credit: T. M. Palmer.

species (e.g., see Palmer et al. 2008). Second, although our study focused on the short-term demographic costs and anti-herbivore benefits of maintaining ant symbionts, there may be long-term thresholds over which incremental damage from herbivores such as cerambycids (the only form of damage that exhibited linear responses to ant abundance) results in fitness decrements. In an eight-year study, host plants with high levels of cerambycid attack grew more slowly and were more likely to die, indicating that cerambycids can significantly affect plant demography at longer time scales (Palmer et al. 2008). Understanding the lifetime fitness impact of cumulative, incremental damage (Letourneau 1998) will require longer-term manipulations, which are currently underway.

Overall, symbiotic *C. mimosae* conferred strong protective benefits to *Acacia* trees, while simultaneously imposing relatively high costs. The functional relationship between ant abundance, their benefits in protecting trees from two important herbivores, and their costs to plant reproduction, suggest that *C. mimosae* achieves higher densities than are optimal for hosts. Although the net benefits of plant ants to their hosts is well established (reviewed in Chamberlain and Holland 2009, Trager et al. 2010), to our knowledge our study is the first to experimentally examine how the costs and benefits to plants of symbiotic ants change with variation in partner abundance. Establishing these functional relationships

for ant–plant and other mutualistic interactions will provide a tool to link the ecological and evolutionary dynamics of mutualism, and will help shed light on the conflicting interests at play within these globally distributed interactions.

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