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PLANT ANIMAL INTERACTIONS

Todd M. Palmer · Truman P. Young
Maureen L. Stanton

Burning bridges: priority effects and the persistence of a competitively subordinate acacia-ant in Laikipia, Kenya

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Abstract Theoretical models suggest that subordinate competitors may rely on strong colonization ability and/or high persistence (e.g., the ability to resist invasion) as a strategy to coexist with competitively dominant species. While strong colonization ability among subordinate competitors has been widely documented, we know less about the role of persistence in facilitating species coexistence. In upland East Africa, four species of acacia-ants (*Crematogaster sjostedti*, *C. mimosae*, *C. nigriceps*, *Tetraponera penzigi*) compete for possession of *Acacia drepanolobium* host trees. Despite a strong dominance hierarchy, the four acacia-ant species coexist at fine spatial scales. Here we present evidence that *T. penzigi*, the least aggressive competitor, modifies host trees in two ways that reduce the probability of aggressive takeover by neighboring colonies. First, *T. penzigi* workers destroy virtually all leaf nectaries on their host trees. Second, *T. penzigi* workers create and maintain entryways into their swollen thorn domiciles that are too small to allow entry by their *Crematogaster* competitors. In a 2×2 factorial experiment, we manipulated nectar availability and swollen-thorn entryway size to determine the influence of these factors on the probability of aggressive displacement by a dominant competitor (*C. mimosae*) in staged conflicts. Addition of artificial nectaries and enlargement of swollen-thorn entryways on *T. penzigi*-occupied trees increased the probability of aggressive displacement of *T. penzigi* by *C. mimosae* from swollen thorns 14-fold and 8-fold, respectively. Further, empty saplings with nectaries destroyed by *T. penzigi* workers were colonized by half as many *C. mimosae* workers as saplings where nectaries were left intact. Our results demonstrate that *T. penzigi*'s unusual strategy of nectary destruction and the maintenance of small entryways in swollen thorns produce priority effects, effectively reducing the probability that *T. penzigi* colonies will be displaced from host trees by more dominant competitors.

Keywords Species coexistence · Ant-plant mutualism · *Acacia drepanolobium* · *Crematogaster* · *Tetraponera*

Introduction

Ecological communities often comprise species that differ in competitive ability. The resulting hierarchies in dominance among competitors raise a question that has preoccupied ecologists for decades: how do subordinate species coexist among dominant competitors? Understanding the mechanisms that underlie the persistence of competitive subordinates remains a major challenge for ecologists, and is among the keys to understanding how biodiversity is maintained.

In communities of sessile organisms, space is often a critical limiting resource. In the face of strong competition for establishment sites, theoretical models suggest that, under certain circumstances, coexistence may be mediated through interspecific tradeoffs in competitive ability, dispersal ability, and longevity (e.g., Tilman 1994, but see Yu and Wilson 2001). Weaker competitors must therefore have high enough rates of dispersal to reach a disproportionate number of open sites (sensu "fugitive models", MacArthur and Wilson 1967; Horn and MacArthur 1972), and/or disproportionately greater persistence in sites where they have established. While tradeoffs between colonization and competitive ability have been documented in many species assemblages (e.g., Werner and Platt 1976; Roughgarden et al. 1988; Gleeson and Tilman 1990; Tokeshi and Romero 1995; Barnes and Clarke 1998), our understanding of the importance of tradeoffs between longevity and competitive ability is less complete (Tilman 1994). Recently, ecologists have begun to focus on the critical role of persistence in the ecology of sessile organisms (reviewed in Bond and Midgley 2001; Young et al. 2001).

T.M. Palmer (✉) · T.P. Young · M.L. Stanton
Center for Population Biology, University of California,
Davis, CA 95616, USA
e-mail: tmpalmer@ucdavis.edu

T.M. Palmer · T.P. Young · M.L. Stanton
Mpala Research Center, Box 555, Nanyuki, Kenya

Once a subordinate competitor has established in a site, its persistence in that site depends upon several factors. Resistance to disturbance clearly plays a role in more variable environments, which are often dominated by assemblages of disturbance-tolerant organisms (Grubb 1977). However, in less severely disturbed environments where post-establishment competition for sites exists, the longevity of a subordinate competitor in a site depends strongly on its ability to resist invasion by stronger competitors. One way that poor competitors may persist in the face of strong competition is through "priority effects", where fitness advantages accrue to the first organism to establish in a habitat (Wilbur and Alford 1985). Priority effects are also implicit in earlier theoretical models of coexistence (e.g. Sale 1977). Demonstrated in a wide range of taxa (e.g., ants, Cole 1983; anurans, Lawler and Morin 1993; spiders, Ehmann and MacMahon 1996; fruit flies, Hodge et al. 1996), temporal priority effects may allow inferior competitors to persist longer in habitats if early establishment gives them advantages over later arrivals, thereby slowing the rate of competitive displacement or exclusion.

Temporal priority effects may feature strongly in the persistence of the plant-ant *Tetraponera penzigi* (Formicidae, Pseudomyrmecinae), a member of a community of acacia-ants residing on *Acacia drepanolobium* in East Africa. In this community, four ant species [*Crematogaster sjostedti* (Formicidae, Myrmecinae), *C. mimosae*, *C. nigriceps*, *T. penzigi*] coexist despite a strong dominance hierarchy among mature colonies in contests for the possession of host trees (*C. sjostedti*>*C. mimosae*>*C. nigriceps*>*T. penzigi* Palmer et al. 2000). These ant species are generally mutually exclusive (only one ant species resides on each tree), and competition for trees is intense; more than 99% of trees >1.0m tall are occupied by ants, and violent interspecific takeovers of host trees by adjacent colonies are commonplace (Palmer et al. 2000), occurring both via the ground and when the canopies of neighboring trees grow together (Stanton et al. 1999). While single *Crematogaster* colonies often occupy multiple trees, *T. penzigi* colonies generally only control a single contiguous canopy (T.M. Palmer and M.L. Stanton, unpublished work).

In a previous study (Palmer et al. 2000), we reported that *T. penzigi* has the lowest ability to aggressively displace other ant species from host trees; in staged pairwise interspecific contests between adjacent colonies for the possession of trees, *T. penzigi* was the least likely to take over contestant colonies of other acacia-ant species. However, most contests involving *T. penzigi* resulted in ties; the more aggressive and expansionist *Crematogaster* spp. did not displace *T. penzigi* from trees in 73% (*N*=33) of contests. By contrast, most contests (88%) among *Crematogaster* species resulted in a clear win or loss (Stanton et al. 1999; Palmer et al. 2000).

The low vulnerability of *T. penzigi*-occupied trees to interspecific takeover appears to result in part from two unique features of the relationship between *T. penzigi* and *A. drepanolobium* that are distinct from the *Crematogaster* spp./*A. drepanolobium* symbiosis. First, the functional nectaries found on the leaves of trees occupied by the *Crematogaster* species are virtually absent on trees occupied by *T. penzigi* (Young et al. 1997; Stanton and Young 1999). Even before leaves are fully expanded, *T. penzigi* appears to actively chew and destroy leaf nectaries on new growth on their trees. Second, a small and narrow body allows *T. penzigi* to create and use entrance holes in swollen thorns that the *Crematogaster* species cannot fit through. When *T. penzigi*-occupied trees are taken over by other species, the invading species must enlarge holes in each swollen thorn by chewing in order to evict and kill the resident ants (T.M. Palmer, personal observation).

We hypothesize that nectary destruction, coupled with strong architectural defense (small entry holes), decrease the benefits and increase the costs of interspecific takeovers of *T. penzigi*-inhabited trees by other acacia-ant species. In combination, these features may afford *T. penzigi* colonies greater persistence in the face of intense competition for host trees by superior competitors.

In this paper, we report results from experiments testing: (1) whether the low number of functional nectaries on trees occupied by *T. penzigi* results solely from active behavior of these acacia-ants; (2) whether unoccupied saplings with intact nectaries are more likely to be colonized by *C. mimosae* workers than saplings on which nectaries were destroyed by *T. penzigi* workers; (3) whether the construction of small entry holes and/or the removal of leaf nectaries by *T. penzigi* decreases the probability of invasion by a dominant competitor, *C. mimosae*.

Materials and methods

Details of the study system can be found in Palmer et al. (2000). Vouchers of the four ant species have been examined by Phil Ward at the University of California, Davis and are on deposit there.

Question 1: do *Tetraponera penzigi* workers destroy the nectar-production capacity of their host trees?

Measurements of nectary condition

When undisturbed by ants, the doubly pinnate leaves of *A. drepanolobium* typically produce a single nectar gland near the base of the primary rachis. To measure the presence and condition of leaf nectaries on trees occupied by different ant species, we surveyed nectaries on randomly chosen branches from 24 trees occupied by each ant species. Trees 1.5–2.0 m in height were selected along randomly oriented transects, alternating between each ant species along the transect. Once a tree was located, we chose the first branch encountered on the eastern side of the tree at a height of approximately 1.25 m. On that branch, we located the first ten leaves, starting from the growing branch tip, and measured the total branch length to the tenth leaf, and the number of leaf nodes on which the first ten leaves were located. The condition of nectaries on each of the first five leaves encountered along the branch was denoted as either active (e.g., nectaries consisting of green or red tissue) or inactive (e.g., either damaged or absent nectaries).

Measurements of nectary destruction by Tetraponera penzigi

To determine experimentally whether the high proportion of missing or inactive nectaries on *T. penzigi*-occupied trees results from direct behavior of the ants, we excluded *T. penzigi* from portions of the canopy for a 7-month period, and then surveyed the condition of nectaries on new growth from ant-removal branches relative to paired control branches on the same tree. We chose 14 trees for ant removal along a N-S transect of approximately 100 m in length. Ants were excluded from portions of the branch by applying a layer of tape covered with Tanglefoot® to the base of a branch, and removing ants present on the branch by cutting open swollen thorns and brushing off the ant occupants. Tanglefoot® barriers were maintained for the duration of the 7-month period. At the end of 7 months, we surveyed the condition of nectaries on the first 20 leaves encountered from the growing tip of the branch and a paired control branch. We classified nectaries as either intact (includes dried nectaries), damaged, or missing.

Question 2: are unmodified *Acacia drepanolobium* saplings more attractive for colonization by *Crematogaster mimosae* workers than saplings modified by *Tetraponera penzigi*?

We conducted an experiment to determine whether the presence of nectaries on unmodified *A. drepanolobium* saplings enhanced colonization by *C. mimosae* workers compared to saplings on which nectaries had been destroyed by *T. penzigi.* We raised the saplings from field-collected seed in an enclosed screenhouse at Mpala Research Center. Seeds were planted in black PVC nursery bags (18 cm×30 cm) filled with "black cotton" soils, a heavy-clay vertisol collected from the site where the field experiment was to be conducted. Saplings were watered every other day and fertilized weekly with Miracle Gro® plant fertilizer. At 12 months of age, saplings were transported to the field to begin the field experiment. In the field, the saplings were watered daily to prevent desiccation.

In the experiment, we chose ten pairs of screenhouse-grown saplings, matched within pairs for size, number of branches and number of swollen thorns. We randomly assigned one sapling within each pair as a "treatment" sapling, and one as a "control". We then wired the longest branch of each treatment sapling to the canopy of an *A. drepanolobium* tree occupied by a mature *T. penzigi* colony. Following the connection of canopies, workers from the mature *T. penzigi* colony were allowed to colonize and destroy the intact nectaries present on the treatment sapling. All treatment saplings remained connected to canopies of mature trees for a period of 7 days, during which time all intact nectaries on all treatment saplings were destroyed.

Control saplings were tied to the same *T. penzigi*-occupied trees as their paired treatment sapling. *Tetraponera penzigi* workers were allowed to colonize these trees, but were removed after several hours before the workers could destroy the saplings' intact nectaries. We then detached canopies of all experimental saplings from canopies of mature trees occupied by *T. penzigi*, and removed all *T. penzigi* workers from the saplings. We cut open all swollen thorns on both control and treatment saplings to ensure that no *T. penzigi* workers remained on experimental trees.

We then randomly selected ten trees 1.5–2.5 m in height occupied by mature colonies of *C. mimosae*, and separated from each other by at least 10 m. At the base of each of these trees, we placed a size-matched pair (one treatment and one control) of experimental saplings at a distance of approximately 20 cm from the base of the mature tree. Using bailing wire, we connected the longest branch of each sapling to the trunk of the focal tree. Following the connection of saplings to the *C. mimosae*-occupied tree, we scanned saplings daily at 2:00 p.m., and recorded the number of *C. mimosae* workers present and the number of *C. mimosae* workers tending nectaries on experimental saplings. Scans were conducted for a total of 8 days.

Question 3: does nectary destruction and small entry-hole size deter aggressive expansion of *Crematogaster mimosae* colonies onto *Tetraponera penzigi*-occupied trees?

To determine whether the small entry-hole size in swollen thorns and low nectar availability reduced the likelihood of takeover of *T. penzigi*-occupied trees by their dominant *Crematogaster* spp. competitors, we experimentally enlarged holes and added nectar to *T. penzigi*-occupied trees. We used a fully crossed 2×2 factorial design, with holes enlarged (yes or no) and nectar added (yes or no) as experimental factors. Trees with no holes enlarged and no nectar added served as controls. Following the manipulations of *T. penzigi*-occupied trees, we then staged experimental contests between these trees and adjacent trees occupied by *C. mimosae*.

We selected 60 pairs of adjacent *C. mimosae*- and *T. penzigi*-occupied trees of approximately the same height (1.5–2.5 m) and canopy volume; pairs were close enough for their canopies to be wired together. Prior experiments in this system (Stanton et al. 1999; Palmer et al. 2000) indicated that canopy contact between host trees occupied by adjacent colonies occurs naturally, and generally incites territorial conflict. Because *C. mimosae* colonies commonly occupy multiple trees, and colony size can influence the outcome of experimental contests for the possession of trees (T.M. Palmer, unpublished work), we recorded the number of trees occupied by each ant colony involved in experimental conflicts. For each experimental tree, we determined the number of adjacent trees occupied by the same colony, following methods given in Hölldobler (1979); conspecific workers from surrounding trees were transferred in swollen thorns to the experimental tree, and the presence of fighting behavior was assessed. When workers transferred to the experimental tree did not fight with the resident ants, their tree of origin was noted as belonging to the same colony.

We then divided these 60 experimental tree pairs into 15 consecutive groups of 4 trees. Within each group, the *T. penzigi*-occupied tree from each tree pair was randomly assigned to one of four treatments: (1) nectar added (N); (2) holes enlarged (H); (3) nectar added and holes enlarged (NH); (4) unmanipulated controls (C). All treatments were applied to the branch of the *T. penzigi*-occupied tree nearest the *C. mimosae*-occupied tree.

Before joining trees of each pair together, we added artificial nectaries to N and NH treatment branches by attaching four 0.5-ml microcentrifuge tubes to the branch with bailing wire. Tubes were evenly spaced every 25 cm from the point where the *C. mimosae* canopy would be attached to a distance of 1.0 m from the point of canopy attachment. Each tube was filled with a 40% sucrose solution, representing approximately 0.29 g sucrose per tube, and was refilled each day. Thus, the total daily sugar addition available on each tree was approximately 0.29×4 tubes/tree=1.15 g sugar per tree per day. This sugar addition is roughly equal to 37% of the daily sugar production (in the form of nectar produced) of a 2.0-m-tall *A. drepanolobium* tree with functional nectaries (Hocking 1970). To control for the effects of the microcentrifuge tubes themselves on tree attractiveness or ant activity, we wired microcentrifuge tubes to trees from control and hole-enlargement treatments, but the tubes were not filled with sucrose solution. Intermittent rains during the duration of the study filled control microcentrifuge tubes with water, which we did not remove. Prior observations in this study system indicated that these acacia-ant species do not use artificial water sources placed on host trees.

Hole-enlargement treatments were applied by drilling two holes large enough for *Crematogaster* entry into each of the first five swollen thorns on the treatment branch of the *T. penzigi*-occupied tree. To test whether the hole-enlargement treatment alone might cause *T. penzigi* ants to abandon drilled swollen thorns, we drilled holes in five galls each on an additional ten *T. penzigi*-occupied trees and monitored the condition of the drilled holes and ant activity in these swollen thorns 48 h later. In addition, we re-surveyed these swollen thorns at weekly intervals for the next 7 weeks, and then cut open all drilled swollen thorns at the end of 7 weeks to survey their contents.

All treatments were applied the day before adjacent canopies were tied together. On the day following the application of treatments, approximately 93% of the drilled holes had been partially or totally occluded with carton by *T. penzigi* workers, so holes on experimental trees were briefly re-drilled immediately prior to canopy connection. In order to initiate competitive conflict, we then attached the nearest branch from both the *C. mimosae*- and *T. penzigi*-occupied tree with bailing wire.

Following canopy attachment, trees were revisited every day for a period of 45 days. Each day, we refilled empty nectaries (N and NH treatments only) and monitored whether either ant species had occupied swollen thorns or branch space on the competitor's tree. When either ant species occupied two or more of the competitor's swollen thorns, the tree-pair was scored as "invaded". Occupation of only a single swollen thorn was not scored as an invasion because the swollen thorn nearest the point of contact was often abandoned by both ants, and subsequent occupation might not reflect a true eviction. We also noted whether any non-drilled holes on swollen thorns on the *T. penzigi*-occupied trees had been enlarged by chewing of *C. mimosae* ants, recognizable by a small, light-colored ring of recently exposed plant tissue around the small entry holes. *C. mimosae* colonies that enlarged entry holes of *T. penzigi*-occupied swollen thorns were scored as having "invested" in the takeover of the *T. penzigi*-occupied tree.

Statistical analyses

All data were analyzed using standard parametrical statistical tests in JMP (SAS Institute 1996). In comparisons of the percent active nectaries on trees occupied by different ant species, we transformed percentage data using the arcsin square-root transformation. We square-root (x+0.5) transformed all count data (number of *C. mimosae* workers present on modified saplings, number of swollen thorns occupied, number of swollen thorns chewed) to satisfy normality requirements. We analyzed sapling colonization data by comparing the mean number of workers on treatment versus control saplings over an 8-day period using paired *t*-tests. Analyses of the number of swollen thorns occupied and chewed by invading ants in the nectar addition and hole-enlargement experiment were conducted using ANCOVA, using the number of trees occupied by each experimental *C. mimosae* colony as a covariate.

Results

Surveys of nectary condition

Trees occupied by *T. penzigi* differed strongly in the condition of their nectaries compared to trees occupied by the *Crematogaster* spp.; fewer than 7% of nectaries on *T. penzigi* trees were active, compared to >50% active nectaries for trees occupied by the three *Crematogaster* spp. (Fig. 1, $F_{3,92}$=16.38, P<0.0001). There was no significant variation among trees occupied by the four ant species in leaf density (branch length per ten leaves, $F_{3,92}$=0.87, P=0.46) or the number of leaves per branch node ($F_{3,92}$=0.37, P=0.77). Accordingly, nectar resources available on trees occupied by *T. penzigi* are a small fraction of those on *Crematogaster*-occupied trees.

Experimental removal of *Tetraponera penzigi* from branches

Removing *T. penzigi* from experimental branches had a dramatic effect on the condition of leaf nectaries (Fig. 2). On branches where workers were present, the proportion of nectaries damaged was 30× greater than on branches from which workers were excluded ($F_{1,26}$=666.1, P<0.0001). Ant-removal and control branches had similar numbers of leaves that did not produce nectaries ($F_{1,26}$=2.04, P>0.16).

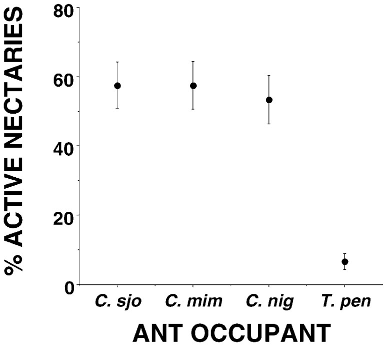

Fig. 1 Percent active nectaries on *Acacia drepanolobium* trees occupied by the four acacia-ant species (*N*=24 trees per ant species). *Error bars* are ±1 SE

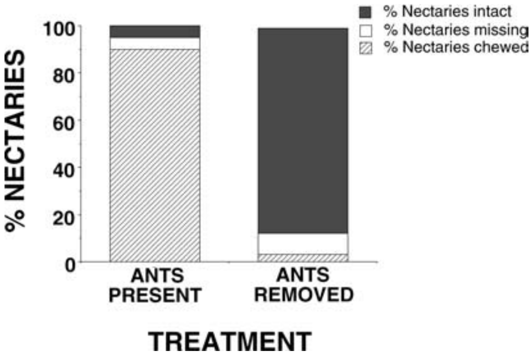

Fig. 2 Condition of leaf nectaries on paired treatment (*Tetraponera penzigi* workers removed) and control (*T. penzigi* workers present) branches on experimental *Acacia drepanolobium* trees (*N*=14 trees)

Colonization by *Crematogaster mimosae* of *Tetraponera penzigi*-modified saplings

Nectary condition affected the probability of *C. mimosae* colonization of experimental saplings. Workers were 50% more abundant on nectaries on control saplings than on treatment saplings on which *T. penzigi* had destroyed nectaries (Fig. 3, paired *t*-test, t=–2.02, 9 *df*, P<0.04). Workers were also approximately 50% more abundant on other parts of the control saplings than on treatment saplings, but this difference was only marginally significant (paired *t*-test, t=–1.59, 9 *df*, P<0.075).

Tetraponera penzigi response to experimental enlargement of entry holes

Within a half-hour of enlarging entry holes on experimental swollen thorns, *T. penzigi* workers began to re-

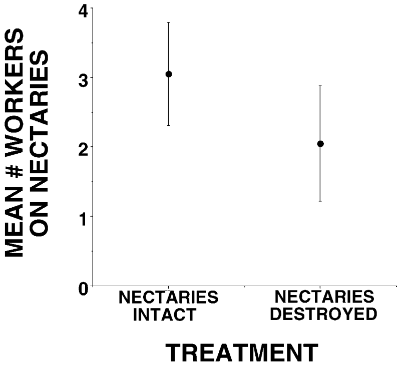

Fig. 3 Number of *Crematogaster mimosae* workers present on paired treatment (nectaries destroyed by *Tetraponera penzigi* workers) and control (nectaries left intact) saplings (*N*=10 saplings per treatment). *Error bars* are ±1 SE

narrow or seal the enlarged holes. Forty-eight hours after enlarging entry holes on five swollen thorns from each of ten *T. penzigi*-occupied trees, all drilled holes had been re-closed, either completely or such that only *T. penzigi* workers could move through them. Drilling did not cause *T. penzigi* workers to abandon swollen thorns, and workers remained in these thorns over the next 7 weeks. At the end of 7 weeks, we cut open thorns to examine their contents. Swollen thorns contained either workers only or combinations of workers, eggs, larvae, pupae, and/or reproductives. In addition, approximately 75% of swollen thorns contained a fine sawdust-like material that appeared to be scraped from the inside of the thorn. This material, which is not found inside the swollen thorns of trees occupied by the three *Crematogaster* species, appears to form the carton material used by *T. penzigi* to re-seal or narrow their entry holes.

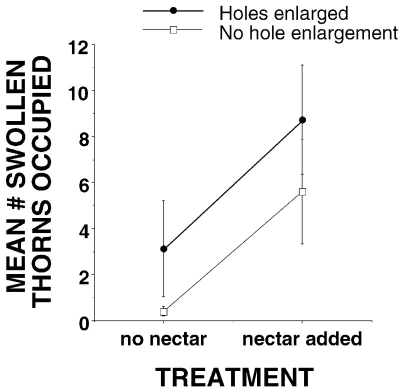

Fig. 4 Number of *Tetraponera penzigi* swollen thorns invaded and occupied by *Crematogaster mimosae* workers (*N*=15 trees per treatment). *Error bars* are ±1 SE

Table 1 ANCOVA on the number of *Tetraponera penzigi* swollen thorns occupied by *Crematogaster mimosae* workers during experimental conflicts (*NTrees* the number of trees in the contestant *C. mimosae* colony). The response variable "number of swollen thorns occupied" was square-root (+0.5) transformed to satisfy normality requirements

Source	*df*	SS	*F*	*P*
Hole enlargement	1	8.97	3.91	0.053
Nectar addition	1	21.68	9.45	0.003
Hole×Nectar	1	4.18	1.83	0.183
*N*Trees	1	0.47	0.21	0.651
Error	55	116.93		
Total	59	155.70		

Effects on swollen-thorn occupation

Both adding nectar and enlarging entrance holes greatly increased the average number of *T. penzigi*-occupied swollen thorns usurped by *C. mimosae* (Fig. 4). *Tetraponera penzigi* were aggressively displaced from 14× more swollen thorns on trees that had been enhanced with nectar resources, and 8× more swollen thorns on trees where entry holes had been experimentally enlarged, although this latter difference was only marginally significant (Table 1). These effects were simply additive; there was no significant interaction between hole enlargement and nectar addition on the number of *T. penzigi*-occupied swollen thorns usurped by *C. mimosae* (Table 1). Re-sealing and/or narrowing of experimentally enlarged entry holes by *T. penzigi* workers may have lessened the efficacy of the hole-enlargement treatment. However, re-opening these narrowed or sealed entryways appeared much easier for *C. mimosae* workers than enlarging small entryways that had not been drilled. The number of swollen thorns *T. penzigi* lost to *C. mimosae* occupation was not significantly influenced by the number of trees in the *C. mimosae* colony (Table 1). Interactions between treatment effects and the number of trees in *C. mimosae* colonies were not significant, and so were dropped from the model.

Effects on "investment" by *Crematogaster mimosae*

When *C. mimosae* workers enlarged the entry holes in *T. penzigi*-occupied swollen thorns to evict the resident ants, we defined this behavior as "investment". Enlarging these holes appeared to entail considerable energetic costs and risks to *C. mimosae* workers. Widening the entry holes of a single *T. penzigi*-occupied swollen thorn generally took between five and seven *C. mimosae* workers approximately 2–4 days. Enlarging *T. penzigi*-occupied swollen-thorn entry holes required the continued presence of the aggressor ant; in the absence of the aggressor, *T. penzigi* workers quickly re-narrowed and/or sealed their entry holes using a carton-like material stored within each swollen thorn. Finally, widening the swollen-thorn entry holes may entail substantial mortality to the *C. mimosae* colony. *T. penzigi* possesses a lethal spatulate sting, and laboratory experiments have demonstrated that a single worker of this species is capable of killing three to four *C. mimosae* workers before suc-

Table 2 ANCOVA on the number of *Tetraponera penzigi* swollen thorns where entryways were enlarged by *Crematogaster mimosae* workers during experimental conflicts. The response variable "number of swollen thorns chewed by *C. mimosae* workers" was square-root (+0.5) transformed prior to analysis to satisfy normality requirements

Source	*df*	SS	*F*	*P*
Hole enlargment	1	0.50	0.14	0.710
Nectar addition	1	19.28	5.38	0.024
Hole×Nectar	1	8.77	2.45	0.124
*N*Trees	1	0.06	0.02	0.894
Error	55	182.69		
Total	59	217.18		

cumbing (unpublished data). On many occasions in the field, we observed *T. penzigi* workers, well defended inside the swollen thorn, stinging and killing *C. mimosae* workers as the latter were attempting to enlarge the entry holes.

Only the addition of an artificial nectar source increased investment behavior by *C. mimosae* workers (Table 2); hole-enlargement treatments did not differ significantly from controls in the number of *T. penzigi*-occupied swollen thorns chewed by *C. mimosae*, nor was there any interaction between hole enlargement and nectar addition (Table 2). The number of *T. penzigi*-occupied swollen thorns chewed by *C. mimosae* workers was not influenced by the number of trees in each *C. mimosae* colony (Table 2). Interactions between treatment effects and the number of trees in *C. mimosae* colonies were not significant, and so were dropped from the model.

Discussion

While symbiotic associations between specialized plant-ants and their hosts have been studied intensively (reviewed in Holldobler and Wilson 1990), we know little about the mechanisms that allow multiple species guilds of plant-ants to coexist within populations of host plants. In the acacia-ant community of *A. drepanolobium*, competition for host trees appears to be very intense; interspecific turnover of occupant ants on host trees can be as high at 7.5% during a 6-month period; unoccupied mature trees are very rare (<<1%) and takeovers are commonly observed in the field (Palmer et al. 2000). Of the four plant-ant species present in this ecosystem, *T. penzigi* has the lowest aggressive displacement ability, winning only 11% of experimentally staged contests for the possession of host trees (Palmer et al. 2000). However, despite an inability to expand its colonies aggressively *T. penzigi* is the second most abundant ant species at our study site, occupying almost 17% of surveyed host trees. How can such a non-aggressive competitor persist in this highly competitive community at such high densities?

As suggested by theory (e.g., Tilman 1994), subordinate species with strong colonization abilities and/or high persistence ability may be better able to coexist with more competitively dominant species. There is evidence that *T. penzigi* possesses strong colonization abilities relative to its *Crematogaster* competitors. In another study, we report that *T. penzigi* is significantly over-represented among foundress queens colonizing available mature trees (Stanton et al. 2002). However, we also found that incipient *T. penzigi* colonies developed far more slowly than their *Crematogaster* competitors (Stanton et al. 2002), potentially putting this species at a competitive disadvantage during the early stages of colony development. Consequently, the mechanisms that slow the rate at which established *T. penzigi* colonies are displaced from their host trees may be critical to the persistence of this species in the habitat and may help to maintain the relatively high species diversity in this system.

High persistence times on host trees may also be especially crucial to the coexistence strategy of *T. penzigi* since their colonies very often only occupy the canopy of a single mature *A. drepanolobium* host tree (Stanton and Young 1999; T.M. Palmer and M.L. Stanton, unpublished data). Unlike other systems in which subordinate ant species may relocate to less desirable sites when evicted from nests by superior competitors (e.g., Fluker and Beardsley 1970), the acacia-ants of *A. drepanolobium* are intensely nest-site limited (Palmer et al. 2000). Consequently, the loss of a host tree implies almost certain death to a *T. penzigi* colony, since this obligately associated species cannot simply re-locate its nest site. By contrast, colonies of the three *Crematogaster* species generally occupy more than one tree (T.M. Palmer, unpublished data), potentially making the loss of a host tree less detrimental to colony longevity.

Results from this study suggest that the unusual strategy of nectary destruction and the maintenance of small entry holes in swollen thorns creates priority effects, effectively reducing the probability that *T. penzigi* colonies will be displaced from host trees by more dominant competitors. Of the two, nectary destruction apparently plays the largest role in slowing the rate at which *T. penzigi* colonies are competitively excluded from host trees, although the carton-building activities of *T. penzigi* workers may have lessened the effectiveness of the hole-enlargement treatment. Our experiments show that supplementing *T. penzigi*-occupied trees with carbohydrate resources, even at relatively low levels (e.g., approximately 37% of a 2.0-m tree's daily production), increased the probability of aggressive displacement of *T. penzigi* by *C. mimosae* from swollen thorns 14-fold. While complete takeovers of *T. penzigi*-occupied trees by *C. mimosae* over the 45-day experimental period were rare (only 7% of experimental conflicts), all occurred on trees where nectar had been artificially supplemented. Field observations suggest that most naturally occurring partial takeovers of *T. penzigi*-occupied trees persist until the aggressor ant has completely taken over (seven of ten cases, T.P. Young, T.M. Palmer and M.L. Stanton, unpublished data), although this takeover process may occur over months or even years (T.P. Young, T.M. Palmer and M.L. Stanton, unpublished data).

In addition, adding nectar to *T. penzigi*-occupied trees significantly increased the incidence of *C. mimosae* "investment" behavior, where workers engaged in the time-consuming and risky process (see results section: effects on "investment" by *C. mimosae*) of enlarging the entry holes of *T. penzigi*-occupied swollen thorns on non-treatment branches and evicting the resident workers. These results suggest that *C. mimosae* colonies make decisions about whether to supplant *T. penzigi* from nest sites based at least in part on the assessment of immediate energy gains available in the vicinity of these nest sites. When carbohydrate resources were supplemented on *T. penzigi*-occupied trees, the competitively dominant *C. mimosae* usually expanded its nest territory to encompass these resources, moving workers and occasionally brood into swollen thorns adjacent to the artificial nectaries. Locating workers more closely to food sources may serve to increase the economic defensibility of those resources by minimizing travel time to and from the foraging area (Hölldobler and Lumsden 1980; Trainello and Levings 1986).

Nectary destruction appears to inhibit the colonization of host trees even in the absence of *T. penzigi* workers; saplings with intact nectaries were colonized by 50% more *C. mimosae* workers than saplings where nectaries had been destroyed by *T. penzigi*. This result suggests that the exploratory behavior of *C. mimosae* workers is mediated by resource availability. We commonly observe "scouts" from mature colonies exploring nearby trees occupied by other colonies, a behavior that may represent assessment of those trees as potential targets for conquest. If the absence of functional nectaries diminishes this exploratory behavior, then *T. penzigi*-occupied trees may be targeted less often for hostile takeover by more dominant competitors.

Other studies have documented plant-ant pruning of both host and neighboring plants, which may serve to reduce light competition (Janzen 1969, 1972) and create firebreaks around host plants (Janzen 1967), eliminate bridges to the host plant over which aggressive ant neighbors might invade (Davidson et al. 1988), and increase living space on the host plant (Yu and Pierce 1998). In an earlier study, we reported that another subordinate competitor in this ant-plant system (*C. nigriceps*, Stanton et al. 1999) prunes host plants in order to reduce the probability of canopy contact with the host trees of aggressive neighbors. In *T. aethiops*, resident ants prune the tips of branches whose internodes are occupied by incipient colonies of conspecific competitors, potentially lowering the nutritional status of the competing colony (Yumoto and Maruhashi 1999). Our results demonstrate that host-plant pruning may also serve to decrease the attractiveness of host plants to aggressive neighbors. This "defense by exploitation" has been noted in rufous hummingbirds (*Selasphorus rufus*), where territory holders preferentially consume resources at territory boundaries to reduce the benefits of exploitation by would-be intruders (e.g. Paton and Carpenter 1984). In the case of *T. penzigi*, the resources are permanently destroyed rather than repeatedly consumed. This behavior may incur little cost to this species beyond the time invested in destroying the nectaries; pseudomyrmecines such as *T. penzigi* lack the specialized digestive adaptations of *Crematogaster* for efficiently processing large volumes of liquid food.

Maintaining small entryways to plant domiciles may be a general feature of the *Tetraponera* genus that affords architectural protection to resident colonies. In the bamboo-dwelling Malaysian ant *Tetraponera* sp. PSW-80 near *attenuata* (F. Smith), colonies nest only in plant internodes with very small entry holes (2×3 mm), allowing this timid pseudococcid-tending species to attain large colony sizes (Buschinger et al. 1994) inside the well-protected bamboo nests. More broadly, other small-bodied ant species may capitalize on their size to coexist with dominant competitors when they occupy nest sites that are inaccessible to those competitors. For example, the tiny *Leptothorax acervorum* coexists with larger and more dominant *Formica* and *Myrmica* competitors in stumps by occupying galleries that are too narrow to admit the other species (Brian 1952). In cases where entryways to nest sites are large enough to allow access by competitors, resident species may block these passages, using body parts (Creighton and Gregg 1954; Wilson and Hölldobler 1985) or materials such as small stones, sand, and twigs (Harkness and Wehner 1977; Hermann 1984). In our study system, the time and energy invested by *T. penzigi* in maintaining very small entry holes in swollen thorns suggests that this attribute provides important insurance against competitive displacement in this highly competitive community.

A. drepanolobium trees occupied by *T. penzigi* are architecturally well defended and yield low short-term energetic returns to would-be invaders. As a consequence of these attributes, *T. penzigi* suffers relatively few losses of host trees to more dominant ant species. For example, while *C. nigriceps* (another competitive subordinate in this system) lost 71% of its host trees to the two competitively dominant species (*C. sjostedti* and *C. mimosae*) in experimentally induced conflicts, *T. penzigi* lost only 18% of conflicts with these dominant species (Palmer et al. 2000). Increased persistence on individual host trees may enable *T. penzigi* to persist more broadly in the ecosystem if colonies can reach reproductive maturity prior to competitive displacement. We are currently conducting studies and developing a matrix-transition model to investigate the quantitative contribution of this increased persistence to the maintenance of the species at the community level.

The territorial defense strategies of ants have been intensively studied, and run the gamut from agonistic interactions at territory boundaries, architectural defense, and the destruction of competitors' nest sites, to the use of chemical repellents, worker castes specialized for fighting, and threat displays (reviewed in Hölldobler and Wilson 1990). In each case these defenses serve to increase the costs to competitors of acquiring the defended resources, whether food resources, foraging territories, or nest sites. In the acacia-ant community of *A. drepanolobium*, the subordinate *T. penzigi* not only employs a fatal sting and architectural defenses to increase the costs to competitors of usurping their host trees, but also decreases the benefits to potential invaders by destroying the short-term carbohydrate production capacity of their host trees. This strategy of defense by exploitation inhibits aggressive takeovers by neighboring colonies, and highlights the intensely competitive nature of this arboreal-ant community.

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