Wars of attrition: colony size determines competitive outcomes in a guild of African acacia ants

TODD M. PALMER

Center for Population Biology, University of California, Davis
and
Mpala Research Center, Kenya

Territorial aggression is a primary mode of population regulation among ants, and frequently leads to the formation of linear dominance hierarchies. However, few experimental studies have investigated the proximate mechanisms that underlie these hierarchies. In this study I examine the mechanisms underlying dominance relationships in interference competition for nest sites in a guild of acacia ants residing on *Acacia drepanolobium*. I show that (1) interspecific conflicts are fought as simple wars of attrition, with mortality ratios among combatant species approximating 1:1, (2) interspecific competitive outcomes, both within and between habitats, closely parallel differences in estimated average colony size among the four acacia ant species, and (3) experimental manipulation of colony size effectively reverses the dominance hierarchy. This is the first study to demonstrate experimentally that size asymmetries underlie dominance relationships in an entire guild of competitors. These results also highlight the contingent nature of ecological dominance in this community. Because dominance is dictated by characteristics of a trait shared by all ant species (colony size), interspecific competitive outcomes may vary if species differ in growth and/or mortality responses to factors such as disturbance or environmental conditions. Contingencies in competitive outcomes among these acacia ants may play an important role in promoting coexistence in this intensely nest-site-limited community.

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In many ecological communities, groups of species compete intensely with one another for shared resources. To understand the dynamics and predict the outcomes of competitive interactions among these species, ecologists frequently conduct experiments to assess interspecific dominance relationships. From these experiments, two contrasting perspectives emerge, each leading to differing expectations of community dynamics and structure, and the mechanisms underlying species coexistence.

In the first view, dominance is considered a species-specific trait. Groups of competing species can be arranged into either linear dominance hierarchies (species A dominates B, A and B dominate C, and so on) or more rarely, intransitive competitive networks (species A dominates B, B dominates C, but C dominates A; Connell 1978). Observations of hierarchical dominance raise questions that have preoccupied ecologists for decades. Why don't

such systems collapse to single-species equilibria comprised solely of the dominant competitor (Gause 1934)? How do these species assemblages coexist? These questions have framed research emphasizing the role of disturbance and other external agents that reduce the abundance of the competitive dominants (reviewed in Pickett & White 1985), allowing for the coexistence of subordinate species despite intense competitive pressures. Alternatively, species may form intransitive competitive networks that reduce the probability of competitive exclusion, but examples of truly intransitive competitive hierarchies are rare (e.g. Buss & Jackson 1979; Kerr et al. 2002).

In the second view, competitive relationships are not strictly linear, but vary in time and space. In this case, dominance cannot be predicted solely by species identity, but rather is context dependent. Increasingly, ecologists are aware that inter- and intraspecific dominance relationships may change with variability in both biotic factors (e.g. life history stage; Stanton et al. 2002) and abiotic conditions (reviewed in Dunson & Travis 1991). In many communities, species coexistence may hinge upon this

Correspondence and present address: T. M. Palmer, One Shields Avenue, Center for Population Biology, University of California, Davis, CA 95616, U.S.A. (email: tmpalmer@ucdavis.edu).

spatial and temporal variability, where competitive relationships between species vary between microsites and/or times (e.g. Chesson & Huntly 1997). Understanding the importance of such variability requires a detailed understanding of the proximate mechanisms that dictate competitive success.

Social insects such as ants offer a unique opportunity to study the mechanisms underlying dominance relationships. Ants are among the most abundant and species-rich taxa on the planet, and competition is a near-ubiquitous feature of ant communities, often resulting in linear dominance hierarchies (Hölldobler & Wilson 1990). Because an individual ant colony can be viewed as a 'superorganism', it is possible to manipulate attributes (including size) of an 'individual' (colony), and examine the impact such manipulations have on competitive success. Recent concern over the ecological and economic impacts of invasive species such as fire ants, *Solenopsis invicta*, and Argentine ants, *Linepithema humile*, has drawn greater attention to the determinants of ecological dominance in ants (e.g. Holway et al. 1998).

The factors that underlie competitive success in ants may differ at the level of the individual or the colony. In one-on-one interactions between ants, attributes such as worker size or the use of chemical defensive/offensive compounds may dictate dominance (Adams & Traniello 1981; Andersen et al. 1991). By contrast, competitive success at the colony level may depend more strongly on disparities in colony size. Experimental studies have demonstrated that the outcome of resource competition at baits may depend on disparities in the number of workers present (Holway 1999; Holway & Case 2001). While studies of competition at baits are common (reviewed in Hölldobler & Wilson 1990), experimental approaches to competition for nest sites or territory are more rare (Adams 1990; Holway & Case 2001). Nevertheless, competition for space is an important feature in many ant communities (e.g. Herbers 1989; Foitzik & Heinze 1998), and correlations between colony size and territory area (Brian & Elmes 1974; Tschinkel et al. 1995) suggest that the ability of ants to displace competitors from territories may depend strongly on numerical disparities.

Across hundreds of thousands of hectares throughout East Africa, *A. drepanolobium* trees are used as nesting sites by four species of specialist-plant ants: *Crematogaster mimosae*, *C. nigriceps*, *C. sjostedti* and *Tetraponera penzigi* (Hocking 1970). *Tetraponera penzigi*, *C. mimosae* and *C. nigriceps* all rely on swollen thorns for nesting space, while *C. sjostedti* generally nests in hollowed-out cavities within the tree's twigs and stem. Colonies of the three *Crematogaster* species typically occupy multiple trees, while *T. penzigi* usually controls only a single contiguous canopy. These ant species are generally mutually exclusive (only one ant species is found on a given tree), and competition for trees is intense; more than 99% of trees taller than 1.0 m are occupied by ants, and interspecific turnover among ants on host trees can be as high as 7% in a 6-month period (Palmer et al. 2000). Violent interspecific take-overs of host trees by adjacent colonies are commonplace, occurring both via the ground and when the canopies of neighbouring trees grow together (Palmer et al. 2000).

Experimentally staged conflicts between these species revealed a linear dominance hierarchy among mature colonies in contests for the possession of host trees (*Crematogaster sjostedti* > *C. mimosae* > *C. nigriceps* > *T. penzigi*), consistent with patterns of naturally occurring transitions on 1770 trees over an 18-month period (Palmer et al. 2000). Anecdotal observations of the experimentally staged conflicts suggest that combatant workers usually engage each other one-on-one, indicating that competitive outcomes may hinge on numerical asymmetries between colonies.

In this paper, I address several questions to determine whether numerical asymmetry in colony size dictates the outcome of competition for nest sites in this guild of acacia ants and underlies shifts in dominance relationships at the landscape scale. First, does the experimentally determined competition hierarchy among the acacia ants reflect differences in average colony size between species? Second, are shifts in interspecific dominance relationships between sites correlated with changes in relative colony size? Third, are outcomes of staged conflicts between species for the possession of host trees predicted by asymmetries in colony size? Alternatively, do competitive outcomes reflect asymmetries in worker size or recruitment speed? Fourth, can the competitive hierarchy be reversed by manipulating relative colony sizes among species? And finally, do ratios of mortality among warring colonies indicate that species differ in fighting ability (e.g. ratio of dead combatants $<$ or $>1:1$), or do these ratios indicate that colony size is the sole determinant of competitive outcomes (e.g. ratio of dead combatants $= 1:1$)?

The acacia ants of *A. drepanolobium* provide a unique system to examine the relationship between colony size asymmetry and competitive outcomes in an entire guild. Because colonies occupy space in a modular fashion (i.e. living in swollen thorns or nest cavities on individual trees and on individual trees in multiple-tree colonies), the relative size of adjacent colonies can be readily manipulated by removing modules. Similarly, inciting territorial conflict between adjacent colonies can be done in a straightforward and realistic manner. Conflict between adjacent colonies naturally occurs when the canopies of host trees grow into one another (Stanton et al. 1999). Artificially attaching canopies of adjacent trees to one another mimics this natural process, and usually induces territorial wars (Palmer et al. 2000). Because all four ant species can usually be found coexisting within a given 0.1–0.2 ha area, it is possible to incite conflicts between all possible pairwise species combinations.

STUDY SITE AND METHODS

Study Sites

This research was carried out at Mpala Research Centre, in the Laikipia District of central Kenya (0°17′N, 37°52′E). All prior studies of this acacia ant community (e.g.

Stanton et al. 1999, 2002; Palmer et al. 2000, 2002; Palmer 2003) have been conducted at a single study site ('primary study site'), occurring on deep, heavy clay, vertisol soils (Ahn & Geiger 1987), where *A. drepanolobium* accounts for over 95% of the overstory. At this site, trees as tall as 7 m occur, but most trees are less than 2.5 m tall (Young et al. 1997; Palmer et al. 2000).

Near the primary study site (<5 km), a second site ('secondary study site') exists on transitional soils, where heavy clay soils intergrade with sandy clay loams (Ahn & Geiger 1987). Located on the edge of an escarpment, this site is considerably more exposed than the primary study site. Preliminary data suggested that this site had lower productivity than the primary study site. At the secondary study site, *A. drepanolobium* trees are somewhat stunted (averaging 0.5 m shorter than those at the primary site), grass cover is lower, and insect abundance in pitfall traps is dramatically lower than at the primary study site (unpublished data). In addition, although all four acacia ant species are found at both sites, there is dramatic variation in their relative abundances. Whereas *C. nigriceps* is the most rare species at the primary study site (occupying approximately 9% of all host trees; E. Wenk, unpublished data), it is the most abundant species at the secondary study site (occupying 53% of host trees; unpublished data). *Crematogaster sjostedti* and *T. penzigi* are relatively uncommon at the secondary study site, each occupying fewer than 5% of host trees. This strong variation in community structure at relatively small spatial scales (thousands of metres) suggests that dominance relationships may differ between the two sites.

Estimating Colony Size in the Four Acacia Ant Species

Because counting the number of workers in a colony requires destructive sampling of entire trees, and because an individual tree may contain thousands or even tens of thousands of ants (Hocking 1970; unpublished data), directly measuring colony size for a large number of colonies was not feasible. As a surrogate, I estimated colony size by measuring the total height of trees occupied by a given colony. To ensure that the total height of trees occupied by a given colony was a reasonable surrogate for colony size, I also measured the number of swollen thorns per tree and the number of workers per swollen thorn on a subset of trees of varying heights (0.8–3.0 m) occupied by *C. mimosae*, *C. nigriceps* and *T. penzigi*. This method was not applicable to *Crematogaster sjostedti*, since this species nests in hollowed-out cavities within *A. drepanolobium*. Dissection of several *C. sjostedti*-occupied trees revealed that the estimated number of workers was much higher than on similar-sized trees occupied by the other three species. I therefore use the total height of trees occupied by *C. sjostedti* colonies as a conservatively low estimate of colony size in this species.

To determine which trees were occupied by a single colony, I used a modification of methods given in Hölldobler (1979). Workers from focal trees were transferred in clipped swollen thorns to all neighbouring trees

within 10 m occupied by conspecifics. I then assessed whether workers from the two trees fought (indicating that trees were occupied by different colonies) or not. Cases where workers from neighbouring trees fought were unambiguous. When neighbours appeared not to fight, I performed a reciprocal transplant to ensure that the trees belonged to the same colonies. Each interaction from the transfer of swollen thorns was observed for approximately 10 min. When colonies occupied more than two trees, I performed a number of reciprocal transplants between different pairs of trees to ensure that identification of same-colony trees was correct. When conflicting results were obtained, all trees were retested until I obtained an unequivocal result. A total of 12, 50, 45 and 15 colonies were measured for *C. sjostedti*, *C. mimosae*, *C. nigriceps* and *T. penzigi*, respectively. Colonies were selected randomly by walking 20 m in a randomly generated direction (0–330°, in 30°-increments), and then locating the nearest host tree occupied by the species to be measured. I measured fewer *C. sjostedti* colonies because their colonies often occupied more than 20 trees, and identifying a single colony usually took at least a full day. Fewer *T. penzigi* colonies were measured because their colonies were almost invariably restricted to one or two trees.

Assessing the Relation between Dominance Rank and Average Colony Size

At the primary study site, I assessed whether dominance rank was related to the average colony size of each species. Dominance rank was derived from a series of previously reported, experimentally staged conflicts between pairs of colonies of all four acacia ant species at the primary study site (see Stanton et al. 1999; Palmer et al. 2000), and calculated as the number of experimental 'wars' won by a species as a proportion of the total number of wars involving that species. This measure of dominance is akin to Schoener's (1983) 'behavioural dominance', where dominant species prevail in interspecific encounter competition due to superior fighting and/or recruitment ability (Davidson 1998).

Patterns of Historical Transitions between *C. mimosae* and *C. nigriceps* at Two Study Sites

Strong differences in the relative abundance of *C. mimosae* and *C. nigriceps* at the primary and secondary study sites suggest that competitive outcomes between species may vary between these two locations. To address this hypothesis, I assessed patterns of historical transitions between *C. mimosae* and *C. nigriceps* on host trees at each study site. Because ant occupants modify their host trees in characteristic ways, it was possible to assess the pattern of historical transitions on trees through careful observation of tree characteristics.

Parallel linear transects were run by two observers, separated by a distance of approximately 10 m. We conducted observations only on trees 1.0–2.5 m in height ($N = 391$, 360 trees at the primary and secondary site,

respectively). Upon encountering each tree, we recorded the present ant occupant of the tree, and then looked for signs of past occupancy by other ants by noting the presence/absence of a series of ant-occupant-specific architectural characteristics. The two most subordinate ant species in this system, *C. nigriceps* and *T. penzigi*, modify tree characteristics in ways that allow an observer to distinguish past occupancy by both species from the two dominant species. *Tetraponera penzigi* workers destroy a portion of axillary buds on trees and chew characteristically small and numerous entry holes (>4) in swollen thorns, while *C. nigriceps* workers create only two larger entry holes at the base of each swollen thorn and destroy almost all axillary buds (Stanton et al. 1999). By contrast, neither of the competitive dominants (*C. sjostedti* and *C. mimosae*) destroys axillary buds on host trees, and both species chew two similar-sized entry holes in swollen thorn bases. I determined past occupancy by these two species using several measures of overall tree condition. While *C. mimosae* nests in the swollen thorns on host trees, *C. sjostedti* workers nest in hollowed-out twigs and stems of *A. drepanolobium* hosts. Consequently, trees that have been occupied by *C. sjostedti* are normally in poor condition and show evidence of prior twig and stem occupation (e.g. dead or dying branches, large entry holes on stems, often with accumulations of pulp material from the tree stem at the outer edge of the entry hole).

Because growth periods on tree branches are separated by easily identified nodal scars, it was possible to standardize comparisons on all trees at both sites to the past four growth seasons. On each focal tree I chose four branches (one from each cardinal direction) and examined architectural characteristics from growth over the past four growth periods. Trees on which determination of past ant occupancy was ambiguous were excluded from the sample.

I tested the reliability of this method on 60 trees from experimentally induced conflicts (Palmer et al. 2000) where transitions occurred at known times over two growth seasons. Using this method, a trained observer successfully predicted both the previous occupants on trees and approximate timing of transitions on 100% of experimental trees.

Measuring Colony Size of *C. mimosae* and *C. nigriceps* at the Two Study Sites

After assessing patterns of historical transitions between ant species, I then measured the number and total height of trees currently occupied by both *C. mimosae* and *C. nigriceps* colonies at the secondary study site. Colony boundaries were assessed in the same manner as described above. I randomly selected focal trees (using methods described above under Estimating Colony Size in the Four Acacia Ant Species) and measured a total of 27 separate colonies for each of the two ant species. I then compared colony size measurements of the two ant species at the two sites using a two-way ANOVA, with species and site as independent variables. I tested whether disparities in average colony size of *C. mimosae* and *C. nigriceps* differed

between the two sites by examining the species × site interaction. Planned contrasts were used to test whether average colony size of the two ant species differed from one another within sites.

Determining the Correlates of Competitive Success in Conflicts between *C. mimosae* and *C. nigriceps*

To experimentally assess whether the outcome of competition between ant colonies was correlated with disparities in colony size, or other factors such as differences in recruitment or worker mass, I staged 10 experimental conflicts between colonies of *C. mimosae* and *C. nigriceps* at the secondary study site. I located 10 pairs of adjacent trees occupied by these two ant species, matched for height and canopy volume. For each focal tree, I determined the number of other trees occupied by the same colony, measured their height, and counted the number of swollen thorns on each occupied tree. In five of these cases, the *C. mimosae* colony was larger than the opponent *C. nigriceps* colony, whereas *C. nigriceps* colonies were larger in the other five conflicts.

I then chose a similar-sized branch from each focal tree to be connected to one another. Prior to the connection of canopies, two observers positioned themselves downwind of the these branches, and counted the number of workers moving across an unmarked line 30 cm from the branch tip. Counts were repeated at 1-min intervals for 5 min, after which the branches were pulled towards one another and connected using bailing wire. Observers then repeated counts at 1-min intervals for the next 5 min, at 5-min intervals for the next 25 min, and 10-min intervals for the next 30 min. After the onset of conflicts, the location on the branch where ants of opposing colonies engaged one another in combat often shifted down one branch from the point of canopy contact, apparently reflecting short-term differences in recruitment strength between warring colonies. When this occurred, both observers shifted their observation points 30 cm away from the location of conflict.

To assess recruitment strength, I calculated the average number of workers recruiting to the interaction after tree canopies had been connected. I also collected 10 workers from each experimental tree at the onset of experimental conflicts to assess average worker mass. These workers were stored in glass vials and transported to the laboratory for freezing and weighing to the nearest 0.01 mg.

Experimentally Staged Conflicts with Manipulated Colonies: Is the Competitive Hierarchy Reversible?

To test experimentally whether competitive outcomes were determined by colony size, I staged conflicts for each of the pairwise combinations of the three *Crematogaster* ant species at the primary study site. I did not stage conflicts involving *T. penzigi*, because this nonexpansionist ant species rarely engages in aggressive interactions

with other ant species, and it alters host tree characteristics in ways that minimize the probability of aggressive take-over by the *Crematogaster* species (Palmer et al. 2002). In a series of 45 experimental conflicts involving *T. penzigi* and *Crematogaster* spp., no take-overs in either direction occurred within the first month of connecting canopies (Palmer et al. 2000; unpublished data).

For each pairwise combination of the *Crematogaster* species, I located 8–10 pairs of adjacent trees ('focal trees'), matched for canopy volume and occupied by the appropriate species. I then determined the number of additional trees occupied by each colony using the methods described above. In each case, the colony of the dominant species (i.e. higher in the competitive hierarchy determined experimentally in Palmer et al. 2000) was larger than the colony of the subordinate species. I then reduced the size of the dominant colony in one of two ways, depending on the identity of the dominant species. In conflicts between *C. mimosae* and *C. nigriceps*, the dominant *C. mimosae* colonies were reduced in size by placing a Tanglefoot sticky barrier (Tanglefoot company, Grand Rapids, Michigan, U.S.A.) at the base of nonfocal trees occupied by the same colony, preventing recruitment of workers from those trees to the focal tree. I reduced the size of the *C. mimosae* colonies until the total number of trees occupied by each colony was one fewer than the *C. nigriceps* colony, and the summed total heights of trees occupied by the dominant was at least 2.0 m less than those occupied by the subordinate species.

In contrast to the other two *Crematogaster* species in this system, *C. sjostedti* nests in hollowed-out cavities within the stem and branches of host trees and often creates entry holes to trees just above ground. As a consequence, it was difficult to create and maintain effective recruitment barriers on the numerous trees in their large colonies. Instead, for conflicts involving *C. sjostedti*, I placed a Tanglefoot barrier at the base of each focal tree, effectively restricting this species to a single tree colony in each conflict. All sticky barriers were carefully maintained during the course of the experiment.

After barriers to recruitment had been established, I pulled individual branches from the two focal trees into direct contact, and attached them using steel wire. After canopies had been attached, I surveyed staged conflicts every 4 h for the first 8 h, and then at 24-h intervals for the next 7 days. At each resurvey, I noted whether active conflict was occurring at the point of canopy contact, and whether either ant species had partially or completely taken over the opponent's tree. Partial take-overs were scored when we found workers of one species patrolling branch systems and occupying some but not all swollen thorns on the opponent's tree. Complete take-overs were scored when only a single ant species could be found on branches and within swollen thorns on both trees. A tie was scored where no continuing conflict between ant species was observed on the focal trees, and no encroachment by either ant onto the competitor's tree was noted. At the end of the 10-day experiment, all conflicts had either resulted in complete take-overs or ties. I concluded the experiment after 10 days, because (1) most conflicts had resulted in take-overs during that time, and (2) I did

not want natural ant mortality to influence the results of these staged conflicts, and focal trees may have been isolated by sticky barriers from the tree(s) where queens resided. Following the 10-day observation period, I removed all sticky barriers and continued to observe conflicts for the next 2 days.

Measurements of Body Mass for the Three *Crematogaster* Species

To determine whether differences in body mass might contribute to competitive differences between the three *Crematogaster* species, I weighed workers from 10 randomly chosen colonies of each species. For each colony, I disturbed resident workers by vigorously shaking a branch, and then randomly selected 10 workers and transported them to the laboratory in glass vials to be weighed. Workers were frozen for 30 min, then weighed on a digital balance to the nearest 0.01 mg. Average worker mass was calculated by taking the mean of the means from the 10 samples per ant species.

Measurements of Mortality for Experimentally Staged Conflicts

I staged additional ant wars between each pairwise combination of the *Crematogaster* species to assess mortality ratios in conflicts between unmanipulated colonies ($N = 8$, 7 and 10 for *C. sjostedti*–*C. mimosae*, *C. sjostedti*–*C. nigriceps* and *C. mimosae*–*C. nigriceps* conflicts, respectively). Conflicts were set up in the manner described above. I then placed a large white sheet on the ground below the point of canopy connection of the two warring ant colonies. After 5 min, I collected and counted all dead or mortally injured workers (immobile because of missing legs, or lacking crucial body parts, such as abdomens or heads) belonging to each species. I then cleared the sheet of all ants and debris, and repeated this procedure two more times. Mortality ratios were then calculated from an average of three separate 5-min counts.

Statistical Analyses

All data were analysed using standard parametrical statistical tests in JMP (SAS Institute 1996). Transformations on data were used where appropriate to satisfy normality requirements (see Figure legends).

RESULTS

Estimates of Worker Number per Tree

Although host trees occupied by *C. nigriceps* had significantly higher average numbers of swollen thorns than host trees occupied by *C. mimosae* or *T. penzigi* (Fig. 1, Tables 1, 2), swollen thorns occupied by *C. nigriceps* contained fewer workers than those occupied by *C. mimosae* (Table 3), and thus, estimated worker number per metre of host tree was similar for these two ant species
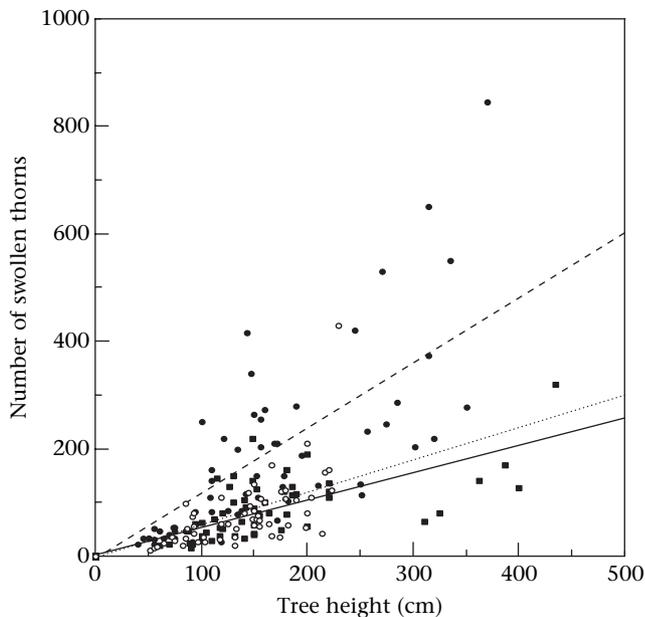
Figure 1. Relationship between host tree height and the number of swollen thorns for trees occupied by the three swollen-thorn nesting ant species. $N = 121$, 80 and 56 trees for *C. mimosae* (-■-), *C. nigriceps* (- -●- -) and *T. penzigi* (···○···), respectively.

(Table 3). Because *C. mimosae* and *C. nigriceps* had similar estimated numbers of workers on trees of a given height, total tree height per colony is an especially sensitive measure of colony size in comparisons between these two species. Because of their twig-nesting habits, colony size of *C. sjostedti* was difficult to estimate. However, dissection of several *C. sjostedti*-occupied trees revealed that the estimated number of workers per tree was higher than that for *C. mimosae* or *C. nigriceps*. Thus, the total height of trees occupied is likely to be a conservatively low estimate of colony size in this species.

Dominance and Average Colony Size at the Primary Study Site

Competitive dominance was strongly correlated with the average colony size of each species, as estimated by the average total height of trees occupied by colonies at the primary study site (linear regression: $R^2 = 0.97$,

Table 1. ANCOVA on the number of swollen thorns on trees of different heights occupied by *Crematogaster mimosae*, *C. nigriceps* and *T. penzigi**

Source	df	SS	*F* ratio	*P*
Ant	2	67.74	3.31	0.04
Height	1	22 119.94	2161.99	<0.0001
Ant × height	2	198.12	9.68	<0.0001
Error	258	2639.66		
Total	263	28 874.00		

*The response variable 'number of swollen thorns' was square-root transformed to satisfy normality requirements. $N = 126$, 81 and 56 for *C. mimosae*, *C. nigriceps* and *T. penzigi*, respectively.

Table 2. Pairwise contrasts from ANCOVA of the average number of swollen thorns on host trees occupied by *Crematogaster mimosae*, *C. nigriceps* and *T. penzigi**

Contrast	Contrast SS	*t* Ratio	*P*
C. mimosae vs *C. nigriceps*	579.49	−7.52	<0.0001
C. mimosae vs *T. penzigi*	3.48	−0.58	0.56
C. nigriceps vs *T. penzigi*	317.51	5.57	<0.0001

*Significance levels for paired contrasts were corrected using the Bonferroni procedure.

$F_{1,3} = 58.87$, $P = 0.017$; Fig. 2). Colonies of the competitively dominant *C. sjostedti* occupied, on average, six times more total tree height than the subordinate *C. nigriceps*, and almost 19 times more tree height than colonies of the subordinate *T. penzigi*.

Changes in Dominance and Colony Size at the Landscape Level

Data from historical transitions on trees indicated that dominance relationships between *C. mimosae* and *C. nigriceps* differed between the primary and secondary sites. These differences were correlated with differences in average colony size in these two areas. Take-overs of *C. mimosae*-occupied trees by *C. nigriceps* were much more likely to occur at the secondary site than the primary site (Fisher's exact test: $P = 0.02$; Fig. 3a). This change in transition probability paralleled a significant disparity in the estimated colony size of each species between the two sites (two-way ANOVA: species × site: $F_{1,136} = 4.06$, $P < 0.05$). While there were pronounced and significant differences in the average size of *C. mimosae* and *C. nigriceps* colonies at the primary study site (planned contrasts: $t_2 = 5.59$, $P < 0.001$), average colony size of the two species did not differ significantly at the secondary study site ($t_2 = 1.44$, NS; Fig. 3b).

Correlates of Competitive Dominance between *C. mimosae* and *C. nigriceps*

All experimentally staged conflicts between *C. mimosae* and *C. nigriceps* resulted in take-overs (6 conflicts won by *C. mimosae*, 4 won by *C. nigriceps*). Asymmetry in colony size was the strongest predictor of competitive success in

Table 3. Estimated number of workers per metre of host tree height for the three swollen thorn-dwelling acacia ant species*

Ant species	Mean no. swollen thorns/m	Mean no. workers/ swollen thorn	Estimated no. workers/ metre of tree
C. mimosae	50.0 (2.60)	65.8 (5.56)	3290
C. nigriceps	100.0 (6.15)	38.4 (5.30)	3840
T. penzigi	53.3 (3.95)	32.3 (5.54)	1722

*Worker counts were based on 70, 42 and 40 swollen thorns from host trees occupied by *Crematogaster mimosae*, *C. nigriceps*, and *T. penzigi*, respectively. Errors (shown in parentheses) are ±1 SE.
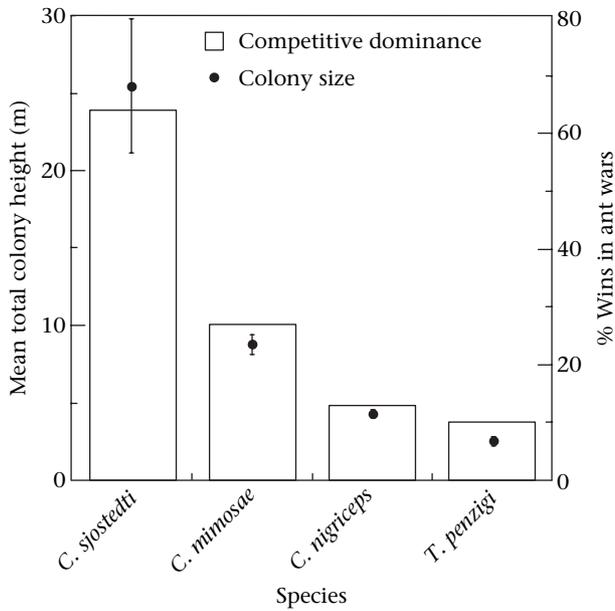
Figure 2. Correlation between dominance rank and average colony size for the four acacia ant species at the primary study site. Dominance rank was calculated from Palmer et al. (2000) as the number of experimentally staged conflicts won by a species divided by the total number of conflicts involving that species (total $N = 33$, 32, 29 and 28 for *C. sjostedti*, *C. mimosae*, *C. nigriceps* and *T. penzigi*, respectively). Average colony size was calculated as the total height of trees occupied by colonies of each species ($N = 12$, 50, 45 and 15 for *C. sjostedti*, *C. mimosae*, *C. nigriceps*, and *T. penzigi*, respectively). For this regression, dominance rank was arcsine-square-root trans-formed, and the total height of trees occupied was log-transformed to satisfy normality requirements. Error bars on average colony size show standard errors.

staged conflicts between *C. mimosae* and *C. nigriceps* at the secondary study site (logistic regression: $\chi^2_1 = 6.01$, $P = 0.014$, significant after Bonferroni correction for multiple comparisons). By contrast, neither differences in average recruitment between colonies (logistic regression: $\chi^2_1 = 0.05$, NS) nor differences in average worker mass between colonies (logistic regression: $\chi^2_1 = 1.64$, NS) were signifi-cant predictors of competitive outcomes.

Experimentally Staged Conflicts between Size-manipulated Colonies

A key result of this study was that outcomes of experimental conflicts were determined by colony size, and not by the identity of combatant species or their position in the putative competitive hierarchy. Reducing colony size of the competitive dominant effectively re-versed the previously established competitive hierarchy (Palmer et al. 2000) in staged conflicts between all ant species pairs tested (binomial test: $P \ll 0.0001$ for all species pairs; Fig. 4). Following the connection of canopies of experimental trees, conflict generally ensued immedi-ately. Workers from the two focal trees met, and some engaged in battle while others rushed to other parts of their host trees, waving their gasters and emanating a pungent alarm pheromone (Wood et al. 2002). In
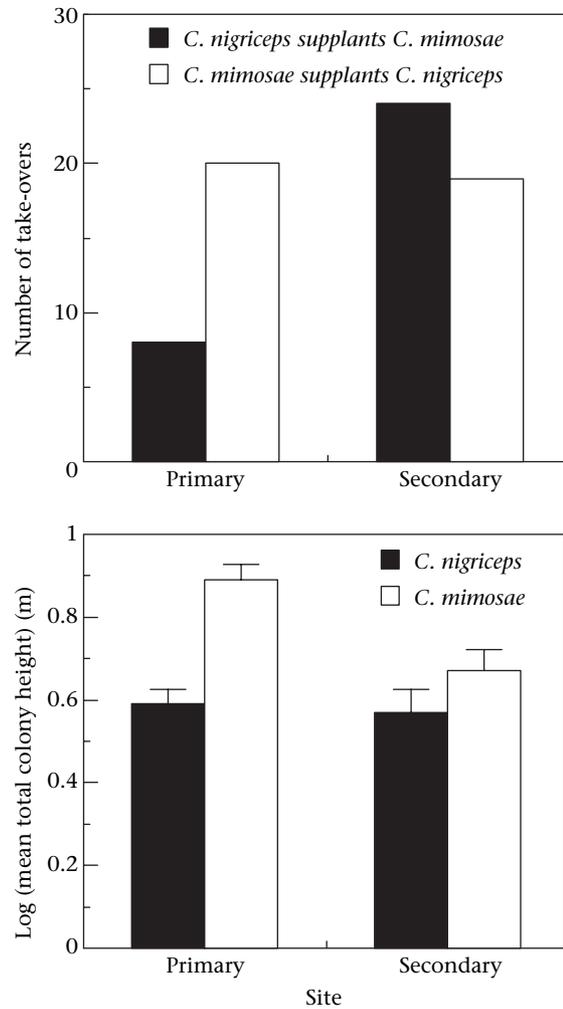

Figure 3. (a) The number of historical transitions in ant occupancy between *C. mimosae* and *C. nigriceps* on host trees at the two study sites. Data were obtained by observing architectural characteristics of trees taller than 1.0 m along randomly oriented transects at the primary and secondary study sites ($N = 391$ and 360 trees, respectively). I used a Fisher's exact test to determine whether the frequency of transitions between *C. mimosae* and *C. nigriceps* differed between study sites. (b) The average total height of trees occupied by *C. mimosae* and *C. nigriceps* colonies at the two study sites. At the primary study site, $N = 46$ and 48 colonies for *C. mimosae* and *C. nigriceps*, respectively. At the secondary study site, $N = 25$ and 21 colonies for *C. mimosae* and *C. nigriceps*, respectively. Error bars show standard errors.

combat, the ants usually engaged each other one-on-one, with fighting pairs clinging tightly to one another, and biting and spraying one another with their gasters. Almost invariably these fighting pairs fell to the ground, and either remained tightly intertwined and fighting, or separated and returned to their host trees. Within 10 min of the initiation of most conflicts, rapid recruitment ensued from other parts of the both focal trees. On trees where Tanglefoot had been applied, workers could be seen attempting to cross the barrier, apparently to recruit colonymates from other trees, but were unable to pass the barrier. Recruitment from nonfocal trees that did not
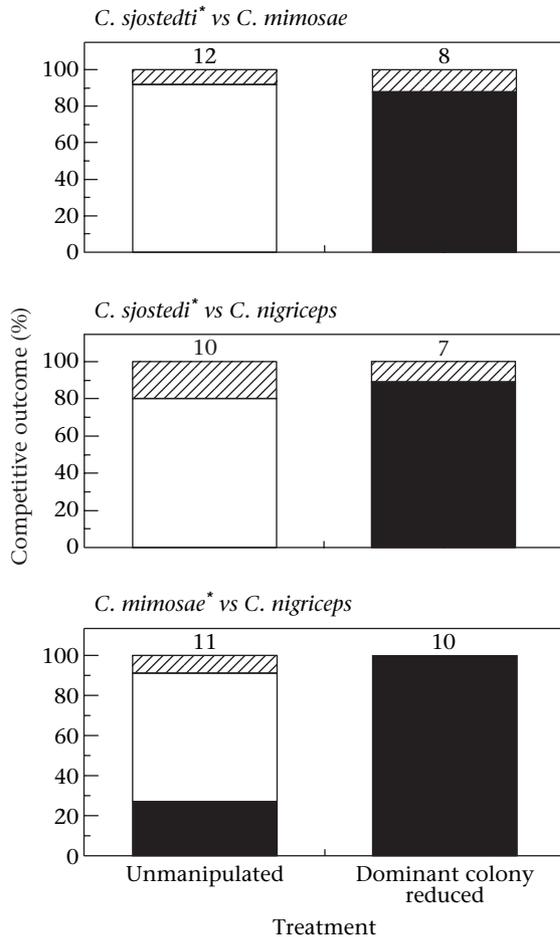
Figure 4. Comparison of competitive outcomes (□: dominant wins; ■: subordinate wins; ▨: tie) of staged conflicts where combatant colonies were unmanipulated or the colony of the competitive dominant was experimentally reduced in size. Results from staged conflicts of unmanipulated colonies are taken from Palmer et al. (2000). The total number of unmanipulated and manipulated conflicts for each species pair is indicated above bars. *Dominant species within a pair.
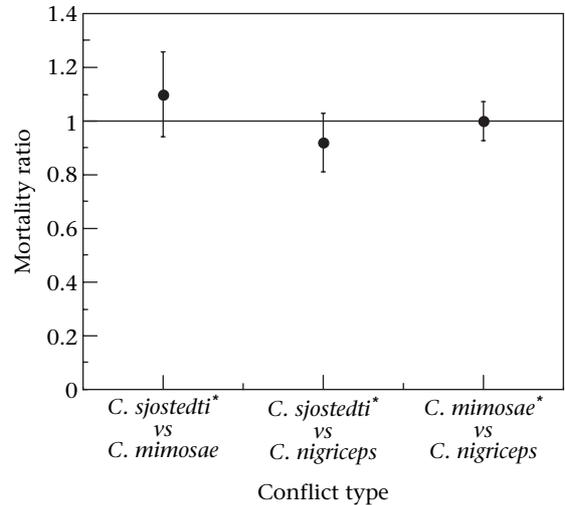

Figure 5. Ratios of mortality between species pairs in experimentally staged conflicts. Ratios were calculated as the number of dead or fatally injured workers of the competitively dominant species of the pair divided by the number of dead or fatally injured workers of the subordinate species. Error bars show ±1 SD. *Dominant species within a pair.

NS), workers of *C. sjostedti* were significantly smaller than the other two *Crematogaster* species (Tukey–Kramer HSD: NS; mean ± SE weight = 7.2 ± 0.50 mg, 16.6 ± 1.20 mg, 14.9 ± 0.87 mg for *C. sjostedti*, *C. mimosae* and *C. nigriceps*, respectively).

Mortality Measurements

A second key result from this study was that colonies of all three *Crematogaster* species suffered strikingly similar mortality during experimental conflicts (Fig. 5). Mortality during conflicts did not deviate significantly from 1:1 for any species pairs (paired t tests: *C. sjostedti*–*C. mimosae* conflicts: $t_7 = 1.82$, NS; *C. sjostedti*–*C. nigriceps* conflicts: $t_6 = -1.68$, NS; for *C. mimosae*–*C. nigriceps* conflicts, $t_9 = 1.02$, NS).

DISCUSSION

Dominance hierarchies have been reported for a number of other ant assemblages (e.g. Vepsäläinen & Pisarski 1982; Fellers 1987; Savolainen & Vepsäläinen 1988; Morrison 1996) and may be mediated by morphological (e.g. size: Fellers 1987), physiological (e.g. defensive compounds: Adams & Traniello 1981; Anderson et al. 1991) and/or behavioural (e.g. reviewed in Hölldobler & Wilson 1990) differences between competing ants. While a number of studies have reported correlations between behavioural dominance and numerical dominance in ant communities (e.g. Hölldobler & Wilson 1978; Lynch et al. 1980; Vepsäläinen 1982; Fellers 1987; Adams 1990; Paulson & Akre 1991; Morrison 1996; Holway et al. 1998; McGlynn 1999), very few experimental studies have addressed how colony size influences interspecific competition within ant guilds (Holway 1999; Holway & Case 2001). Three

have sticky barriers generally began to occur within 20 min of canopy connection. In two cases, worker densities on focal trees appeared to be extremely low, and workers were not present on branches that had been experimentally connected. In these cases, no conflict occurred during the experiment.

Competitive take-overs generally occurred within 24–48 h of canopy connection. Following the 10-day experiment, sticky barriers were removed from trees of dominant colonies. In most cases (20 of 25), colonies of the dominant species, free to recruit workers from previously barricaded trees, recaptured their host trees from the subordinate species within 48 h after removal of sticky barriers.

Measurements of Worker Mass

While *C. mimosae* and *C. nigriceps* workers did not differ significantly in average wet mass (Tukey–Kramer HSD:

lines of evidence from the present study clearly demonstrate that competitive outcomes among this guild of African acacia ants are determined by numerical advantage at the two sites studied. First, interspecific dominance relationships were strongly correlated with variation in estimated average colony size between species at both the primary and secondary study sites. Second, experimentally staged conflicts showed that wars between ant colonies are won through a process of attrition; competitive outcomes in experimental conflicts between *C. mimosae* and *C. nigriceps* were predicted by colony size asymmetry, but not by short-term differences in recruitment ability or differences in worker mass. Larger colonies won conflicts even if the opponent colony had larger workers or more rapid initial recruitment. Consistent with these observations, reversals in dominance relationships among all the *Crematogaster* species were consistently obtained when colony size was experimentally manipulated. Finally, mortality in experimental conflicts was equivalent for all pairwise combinations of the *Crematogaster* species. These results provide strong evidence that the outcome of interspecific competition for nest sites in this community is determined primarily by numerical advantage, rather than species-specific fighting abilities. This is the first study to provide experimental evidence that colony size is direct predictor of success among an entire guild of ants competing for nest sites.

Dominance hierarchies provide a useful and convenient conceptual framework for characterizing competitive interactions between ant species. However, viewing dominance hierarchies as strictly linear may be misleading, because of the implication that coexistence is only possible when external agents (e.g. disturbance, environmental harshness) reduce the abundance of dominant species, or mitigate the importance of species interactions between dominants and subordinates. Theoretical models have challenged this perspective, suggesting that competitive outcomes can be contingent; environmental variation can change the outcome of species interactions without lessening the importance of the interactions themselves (Chesson & Huntly 1997; Chesson 2000). Consistent with these predictions, recent empirical studies have shown that competitive outcomes among ant species may change with variation in factors such as resource type (e.g. Sanders & Gordon 2003) and temperature (e.g. Cerdá et al. 1997). The present study adds to this literature, suggesting that spatial and temporal variation in colony size may result in differences in competitive contingencies between sites. In a previous study (Palmer et al. 2000) we reported that, while the majority of interspecific transitions in ant occupancy on host trees are congruent with the putative dominance hierarchy, competitive reversals are not uncommon, occurring in 16% of all experimental transitions and 36% of all naturally occurring transitions. Results from this study illustrate a potential mechanism for these competitive reversals in the acacia ant community; because competitive outcomes depend strongly on relative colony size, a larger colony of a normally subordinate species should win contests for the possession of host trees against smaller colonies of normally dominant species. These competitive reversals may play a role in facilitating species coexistence in this intensely nest-site-limited community.

A number of environmental conditions may differentially favour colonies of subordinate species relative to dominant species within this community. For example, prior experiments (Palmer 2003) and results from this study suggest that the four acacia ant species respond differently to gradients in resource availability. In a previous study conducted at the primary study site, I used experiments and stable isotope analyses to show that the competitively dominant *C. sjostedti* and *C. mimosae* were more successful at exploiting higher resource densities in productivity 'hotspots', whereas the subordinate *C. nigriceps* and *T. penzigi* were more successful in areas of lower productivity, perhaps resulting from a higher tolerance to low resource conditions (Palmer 2003). Consistent with these findings, results from the present study show that while *C. nigriceps* had the lowest rank abundance among the acacia ants at the primary study site (occupying 9% of host trees), it had the highest rank abundance (53%) at the secondary site only 5 km distant, where productivity correlates (invertebrate densities, vegetative cover, and *A. drepanolobium* growth) are markedly lower (unpublished data). Environmental conditions at the secondary study site appeared to differentially favour colonies of the subordinate *C. nigriceps*, lessening the disparity in average colony size found between this species and *C. mimosae* at the primary study site. As a consequence, historical transitions where *C. nigriceps* supplanted *C. mimosae* were significantly more likely to occur at the secondary site, whereas *C. mimosae* was clearly dominant to *C. nigriceps* at the primary study site. Site-dependent variation in competitive outcomes may lead to intransitive competitive hierarchies at larger spatial scales, enhancing overall diversity (Sanders & Gordon 2003).

A second environmental variable that may differentially influence colony size among these species is fire. Fire is the dominant form of disturbance in *A. drepanolobium* savannas, and historically these systems may have burned as frequently as every 5–10 years (N. J. Georgiadis, personal communication). The competitively subordinate *C. nigriceps* uses highly effective behavioural strategies to avoid fire, resulting in very high survivorship following these intense, periodic disturbances (unpublished data). Higher survivorship, coupled with strong colonization abilities shown by both subordinate *C. nigriceps* and *T. penzigi* (Stanton et al. 2002) may give these species crucial numerical advantages against incipient colonies of the more dominant *C. mimosae* and *C. sjostedti* spp. (also see Davidson et al. 1991; Longino 1989; Hahn & Tschinkel 1997), allowing these normally subordinate species to dominate habitats that are frequently disturbed. Consistent with this hypothesis, anecdotal observations (T. P. Young and T. M. Palmer, personal observations) indicate that *C. nigriceps* and *T. penzigi* are community dominants in several highly disturbed sites elsewhere in Kenya. Experiments examining the influence of fire on both short- and long-term community dynamics of these acacia ants are underway.

Because colony size dictates competitive outcomes among the acacia ants, life history traits that increase

colony growth capacity should be primary determinants of a species' competitive performance within this guild. Several life history differences among the acacia ants are likely to be particularly important in this regard. First, the competitively dominant *C. sjostedti* and *C. mimosae* are strongly polygynous; an excavation of two trees of a 23-tree *C. sjostedti* colony revealed seven egg-laying queens, and a four-tree *C. mimosae* colony was found to have four egg-laying queens (unpublished data). By contrast, dissections of a number of entire *C. nigriceps* and *T. penzigi* colonies have yielded only single egg-laying queens (6 colonies and 5 colonies, respectively; T. Palmer & M. Stanton, unpublished data). Queen number and colony size are positively correlated among other ant species in both interspecific (reviewed in Hölldobler & Wilson 1990) and intraspecific (Komene et al. 1999) comparisons. In addition, polygyny (e.g. colonies with multiple egg-laying queens) is often associated with competitive dominance among ant species (McKey 1984; Hölldobler & Wilson 1990; Balas & Adams 1996).

A second factor underlying interspecific differences in average colony size is the allocation of reproductive effort to workers versus alate reproductives. Whereas foundress queens of *C. sjostedti* and *C. mimosae* are under-represented relative to their local abundance on large, empty trees (representing hosts of potentially high value), foundress queens of *T. penzigi* and *C. nigriceps* colonies are significantly over-represented (Stanton et al. 2002). These results suggest that *C. nigriceps* and *T. penzigi* may invest disproportionately more resources into the production of foundress queens. *Crematogaster nigriceps* and *T. penzigi* may 'trade off' the production of workers for the production of foundress queens, increasing colonization ability at the expense of competitive ability of mature colonies for the possession of nest sites. Trade-offs in colonization and competitive ability have been observed in a wide range of taxa (e.g. plants: Platt & Weiss 1985; Tilman 1994; benthic invertebrates: Grosberg 1988; Barnes & Clarke 1998; insects: Denno et al. 1989), and have been suggested as an important force maintaining species coexistence in ant communities (Hölldobler & Wilson 1990; Davidson & McKey 1993; Stanton et al. 2002). Results from this study suggest that increased allocation to the production of workers can directly influence the competitive performance of colonies in this system.

Third, differences in colony foraging and energetics are likely to be important determinants of colony size in these species. While all three *Crematogaster* species have access to carbohydrate-rich nectar resources on host trees, only the dominant *C. sjostedti* and *C. mimosae* tend exudate-producing scale and homopteran insects. Excess carbohydrates harvested from these insect associates may potentially be used to fuel activities that increase colony growth rates, such as foraging for nitrogen-rich resources (e.g. insect parts) on host trees (Davidson 1997). Consistent with this hypothesis, the three *Crematogaster* species differ strongly from one another in their ability to locate and recruit to protein-rich tuna baits placed on the ground near host trees, and in their ability to displace ground-dwelling ant competitors from these baits (*C. sjostedti* >

C. mimosae > *C. nigriceps*; Palmer 2003). Differential success in off-tree foraging ability among these species may also reflect variation in colony size, inherent differences between species in food acquisition or defence, and/or variability in energetic allocation to other activities (e.g. tending nectaries, patrolling, tending brood).

The primacy of colony size in determining competitive performance in this guild may also help to explain an unusual life history trait of the subordinate *C. nigriceps*. Workers of this species destroy lateral and terminal meristems on branches of *A. drepanolobium* (Young et al. 1997), increasing branch number and canopy density on their host trees (Stanton et al. 2002). While this pruning behaviour decreases the probability of canopy contact with adjacent colonies (Stanton et al. 1999; see also Davidson et al. 1988), it also results in higher swollen thorn densities (T. Palmer, T. Young & M. Stanton, unpublished data), thereby potentially increasing worker carrying capacity on individual trees (see also Yu & Pierce 1998). Higher colony densities on host trees may increase the defensibility of *C. nigriceps* nest sites, potentially comprising an important part of the persistence strategy of this competitively subordinate species.

Elsewhere in East Africa, there exists strong intersite variation in the relative abundances of these acacia ants (Hocking 1970; unpublished data). Whether this geographical variation in community structure can be attributed to colony-size-mediated changes in dominance relationships or other factors (e.g. dispersal limitation, abiotic conditions) is not yet known. For the two sites examined in this study, colony size and not species-specific fighting or recruitment ability, dictated the outcome of interspecific competition for nest sites between these acacia ants. Because colony size is a trait that can vary both in time (e.g. life history stage, Stanton et al. 2002) and space (e.g. between microhabitats, Palmer 2003) within this guild, these results underscore the importance of spatial and temporal variability in the maintenance of biodiversity.

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