Research article

Ecological barriers to early colony establishment in three coexisting acacia-ant species in Kenya

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Abstract. In black cotton uplands in East Africa, four symbiotic acacia-ant species compete for possession of a single swollen thorn tree species, *Acacia drepanolobium*, and yet coexist at fine spatial scales. Three of the four ant species produce independent foundress queens that establish colonies claustrally within swollen thorns, most often on small saplings. We conducted surveys of such saplings at two sites in 2001 and 2004, and examined foundresses and incipient colonies within their swollen thorns to determine what factors influence their success. Competition among foundresses for nest initiation sites was intense, with an average of over one founding attempt per swollen thorn in all samples, and with living and dead queens significantly hyper-dispersed among available thorns. Combat with other foundresses was the most common cause of death among claustral queens, especially for *Tetraponera penzigi*. In interspecific battles for nest initiation sites, *T. penzigi* was dominant over *Crematogaster nigriceps* and *C. mimosae*, and *C. nigriceps* won over 80% of its contests with *C. mimosae* foundresses. For singleton foundresses, brood parasitism by the braconid wasp *Trigastrotheca laikipiensis* typically results in the death of the entire ant brood. Host queens defend parasite larvae, pupae and eclosed adults, apparently unable to distinguish the wasps from legitimate offspring. Rates of brood parasitism were as high as 15–20% for incipient colonies of both *Crematogaster* species, but were extremely low for *T. nigriceps* in all samples. Although *T. penzigi* and *C. nigriceps* foundresses are always solitary, approximately 18% of claustral *C. mimosae* colonies contain cooperating pleometrotic queens. For unparasitized, claustral *C. mimosae* colonies, brood production per queen did not differ between solitary and cooperating foundresses. However, the per-capita risks associated with parastitism were reduced for pleometrotic queens.

Introduction

Many attributes of ant communities, including local species diversity, patterns of intraspecific and interspecific nest spacing, and genetic structure within populations hinge on the successes and failures of incipient colonies (Gordon and Kulig, 1996; Hahn and Tschinkel, 1997; Yu and Davidson, 1997; Cole and Wiernasz, 2002). Most young colonies fail to establish (Perlman, 1992; Punttila and Haila, 1996; Hahn and Tschinkel, 1997; Jerome et al., 1998; Stanton et al., 2002; Nery and Vasconcelos, 2003), and so identifying the ecological factors that cause these propagules to fail is important to understanding the dynamics of ant communities and populations.

Just as exploitative and interference competition strongly influence the spatial distribution, survival, growth, and reproduction of established ant colonies (Cole, 1983; Cushman and Addicott, 1989; Gordon and Kulig, 1996; Chan et al., 1999), competition can also operate during the early phases of colony founding in both terrestrial ants and plant-ants. This early-phase competition takes four principal forms: 1) exploitative competition among mated queens searching for limited nest sites (Pfennig, 1995; Foitzik and Heinze, 1998; Stanton et al., 2002); 2) direct interference competition among queens fighting over nesting sites (Adams and Tschinkel, 1995; Federle et al., 1998b; Stanton et al., 2002); 3) extirpation of incipient colonies by workers of established colonies nearby (Pfennig, 1995; Federle et al., 1998a; Jerome et al., 1998); and 4) fighting between newly emerged workers of neighboring, incipient colonies. This last mechanism appears to be especially common in plant-ants, as myrmecophyte saplings are often colonized by many queens

whose workers subsequently fight for exclusive possession of that host-plant (Janzen, 1975; Davidson et al., 1989; Longino, 1991; Perlman, 1992; Vasconcelos, 1993; Yu and Davidson, 1997; Yumoto and Maruhashi, 1999).

These density-dependent impacts of early competition may be ameliorated in ant species where queens co-habit nest sites during the early stages of colony founding, a phenomenon known as pleometrosis (Rissing and Pollock, 1988; Sommer and Hölldobler, 1995). Groups of queens often collectively produce more brood than singleton queens (Mintzer, 1979; Nery and Vasconcelos, 2003), and may have a greater ability to fend off aggressive ant workers (Jerome et al., 1998). However, pleometrotic foundresses often become antagonists later, and in many cases, only a single queen survives (Bernasconi and Keller, 1999). Identifying the ecological costs and benefits of pleometrosis during the early stages of colony establishment continues to be a goal for both theoretical and empirical ecologists (Bartz and Hölldobler, 1982; Nonacs, 1989, 1993).

Although competition has received by far the most attention from ant ecologists, natural enemies other than competitors may also have significant impacts on ant colony success at multiple stages of development (Feener, 2000). An astonishingly diverse array of parasites is known to infest mature ant colonies (tabulated in Hölldobler and Wilson, 1990), and in some cases these parasites are known to reduce colony performance (Feener, 1981, 2000; Morrison, 1999; Mehdiabadi and Gilbert, 2002). Given the impact parasites can have on mature ant colonies, it seems likely that parasites could also significantly affect foundress ant queens and their brood, but there are few data on this issue.

To document the impacts of competition, cooperation, and parasitism on early phases of colony establishment, we studied several species of acacia-ants that compete intensely for exclusive possession of the same species of swollen thorn acacia, but which nonetheless co-exist within upland, black cotton habitats in Kenya (Hocking, 1970; Young et al., 1997; Palmer et al., 2003). Although there are four acacia-ant species within this guild at our study sites, one species rarely if ever produces independent foundress queens, and so the other three guild members are the focus for our analysis. Foundress queens of all three species seek out small saplings of their host tree (*Acacia drepanolobium*) that possess swollen thorns, but which have not been fully occupied by workers of a mature colony (Stanton et al., 2002). After chewing an entry hole into a swollen thorn, foundresses seal themselves within the nesting chamber while producing their first brood (Hölldobler and Wilson, 1990; Brown and Bonhoeffer, 2003). By sampling such claustral colonies on saplings from two study sites in two different years, we addressed the following questions.

1) To what extent do foundress queens experience exploitation and/or interference competition for potential nest initiation sites?
2) Do the foundress queens of the three acacia-ant species differ in their ability to compete for nest initiation sites?
3) What are the major sources of failure experienced by foundresses of the three focal species? Do these barriers to establishment differ between species?

4) Does parasitism of claustral queens and their brood significantly reduce the establishment success of incipient colonies? To what extent do the effects of parasitism differ between singleton queens and pleometrotic foundress groups?

Natural history of the study system

Our surveys were carried out at the Mpala Research Centre (Mpala) in the Laikipia District of Kenya ($0^E17'$ N, $37^E52'$ E) at approximately 1800 m elevation. Black cotton soils develop in poorly drained upland plateaus throughout East Africa and are common at Mpala. Throughout Laikipia, black cotton soils support a species-poor bush savanna vegetation, in which a single species of swollen thorn acacia (*A. drepanolobium*) dominates the canopy (Taiti, 1992; Young et al., 1998). *A. drepanolobium* branches are densely armed with stipular thorns up to 60 mm long. A variable fraction of these stipular thorn pairs (ca. 5–20 %) have a hollow, basal swelling which is used as a nesting chamber by symbiotic ants. *Acacia drepanolobium* leaves bear 1–3 extrafloral nectaries along their central rachis, but do not produce food bodies.

At sites near Mpala, the four common acacia-ant species that occupy *A. drepanolobium* (Young et al., 1997) wage frequent battles over host trees (Palmer et al., 2000). Although any given tree is dominated by a single acacia-ant colony, multiple ant species typically coexist within this habitat at fine spatial scales. Experiments and direct observation indicate that host trees are a limiting resource for both mature colonies and colonizing foundress queens (reviewed in Palmer et al., 2003).

The four species of acacia-ants in this system have sharply contrasting life histories. *Crematogaster sjostedti* is a competitive dominant in fertile sites, especially near termite mounds (Palmer, 2003), and has colonies spanning multiple trees and containing many laying queens. Colonies of *C. sjostedti* appear to propagate by budding and fission, as we have never encountered a truly independent foundress queen of this species. Independent foundresses of the other three acacia-ant species are present at high densities throughout the study area. Two species which are competitively subordinate in competition between mature colonies for *A. drepanolobium* trees (*Crematogaster nigriceps* and *Tetraponera penzigi*) are strictly monogynous, and their foundress queens are always solitary. In *Crematogaster mimosae*, small colonies appear to be mostly monogynous, but large, multi-tree colonies may have multiple laying queens. Foundresses of this last species sometimes occur in pleometrotic groups of up to seven queens and brood within a single swollen thorn.

For the three focal species within this acacia-ant guild, colony founding is strictly claustral. Mated queens search for unoccupied swollen thorns, usually on small (< 0.6 m) saplings of *A. drepanolobium*. After discovering a promising swollen thorn, the foundress chews a small entrance hole through the sclerotized exterior of the swollen thorn chamber, a process that may take up to two hours. Once inside the

hollow swollen thorn chamber, the foundress typically seals her entrance hole. *T. penzigi* foundresses make a tight seal out of scrapings from the interior of the swollen thorn, whereas the two *Crematogaster* species manufacture seals of coarser texture, incorporating thorn scrapings, *Acacia* leaflets, and parts of dead insects into the plug. Pleometrotic groups of *C. mimosae* sometimes have openings that are incompletely sealed, perhaps because late-arriving foundresses enter through existing seals and do not repair them.

Some claustral colonies of these acacia-ants are attacked by a previously undescribed braconid wasp, *Trigastrotheca laikipiensis* (Quicke and Stanton, in press). Undetected by the foundress, *T. laikipiensis* larvae consume eggs and/or larvae of the host queen, and pupate as cocoons within the nest chamber. Parasitized ant foundresses continue to protect wasp parasites as pupae, and even after they eclose as adults within the claustral chamber.

Materials and methods

Sampling and observation methods

All the data reported in this paper were obtained by destructive, "snapshot" sampling of swollen thorn domatia on saplings of *A. drepanolobium*. In 2001 and 2004 we searched within two sites for saplings bearing swollen thorn domatia potentially occupied by foundress queens. The two sampling sites, separated by approximately 3 km, have markedly different acacia-ant communities. At the Exclosure site (near the Kenya Long-term Exclosure Experiment, Young et al., 1998), all four species of acacia-ants within the guild are common. *A. drepanolobium* trees within this area can be as tall as 6 m, although the majority of trees are ≤ 3.5 m in height. Overall, more trees are occupied by *C. mimosae* than by any other species in this area (Young et al., 1997; Palmer et al., 2000). At the second sampling site (called "Mudhole" in honor of a road segment that becomes impassable in wet weather), *A. drepanolobium* trees appear to have stunted growth, and almost no individuals are > 2 m tall. Both *T. penzigi* and *C. sjostedti* colonies are rare at Mudhole, whereas colonies of *C. mimosae* and *C. nigriceps* appear to be co-dominant.

In June–July 2001 and 2004, we searched exhaustively within ca. 5 m of transects (50–150 m in length) through both sampling sites to find small saplings bearing swollen thorns, but which were not patrolled by ant workers. Swollen thorn domatia were inspected, and all those which could potentially serve as nesting chambers by foundress queens were collected. Swollen thorns begin as green, soft swellings, then mature into reddish-black, hardened structures, and later become grey and brittle with age. Foundress queens will only occupy thorns that are hardened, but not brittle. If there were openings in the collected thorns, we sealed the opening with window caulking, and then placed thorns into a refrigerator for up to 2 days. Overall, we collected and opened over 1500 swollen thorns for this study, of which 1216 were deemed potentially occupiable for foundress queens.

Each collected swollen thorn was cut open and examined under the microscope. A number of these thorns were occupied by other insects, including several species of spiders and moth larvae. Living foundresses never occupy domatia with spiders, and rarely co-occur with the moth larvae, and so these thorns were scored as "unavailable" for ant colony establishment. In available thorns, foundress queens, both alive and dead, were counted and identified to species. For most thorns, ant eggs, larvae, pupae, and (in some cases) young nanitic workers were counted. We also examined the brood carefully at high magnification to search for larvae of the brood parasitic wasp. We could apparently not distinguish wasp eggs or very early instar wasp larvae from those of their ant hosts, but middle-to-late instar wasp larvae could be distinguished by their shape and by the fact that they could be observed sucking the fluids from

ant eggs and larvae. Wasp cocoons and eclosed adults were counted. We partially re-sealed some of the parasite-containing thorns, keeping the foundress queen and any remaining brood inside, to rear out some of the wasps for identification and to observe responses of foundresses to the parasite.

Statistical and analytical methods

All analyses, unless otherwise indicated, were conducted using SAS v. 8 analysis software (SAS-Institute, 1992).

To test for exploitation competition among foundress queens searching for nest chambers, we compared the observed distribution of the number of foundresses per available swollen thorn to the Poisson distribution that predicts the distribution of queen number per thorn based on a model of random occupation and the mean number of queens per thorn (also see Stanton et al., 2002). If swollen thorns represent a limited resource for which foundresses compete, then one expects to find that queens are hyper-dispersed, with fewer empty thorns and more thorns colonized by single queens than expected relative to the Poisson expectation. Chi-squared tests were used to test for significant deviations from the random expectation. We included both living and dead queens found within thorns in the analysis, since both classes represent colonization attempts. Samples for each year and each site were analyzed separately, since each represents a different colonization pool. To minimize low-frequency cells in the analysis, we pooled thorns containing ≥ 5 (living + dead) foundresses at the Exclosure site, and pooled thorns containing ≥3 foundresses at the Mudhole site.

In this acacia-ant guild, multiple foundress queens commonly attempt to colonize a single swollen thorn (Stanton et al., 2002). To test for variation among ant species in their ability to fight for nest initiation sites, we focused on thorns with two different species of foundress inside (n = 90 foundresses, pooled across both years and sites). Foundresses of different species never tolerate one another, and typically fight to the death. In some cases, we found queens still engaged in inter-specific combat within collected thorns. These were not included in our analysis, as the outcome of the battle could have been altered by our collection methods. Similarly, a few thorns contained more than two species of foundress; these were also excluded from our analysis, since the species pairs involved in interspecific battles could not be determined with certainty. For thorns with two queen species present, each foundress was scored as a winner, if alive, and a loser if dead (also see Stanton et al., 2002). For each pair-wise species comparison, we used a two-tailed binomial test (Zar, 1996) to determine whether the number of winners recorded for each species differed significantly from the 1:1 ratio expected under the null hypothesis of equal fighting ability.

To compare sources of mortality for foundresses of the three focal species, we assigned a likely cause of death based on the tableau we found within each sampled swollen thorn. Dead queens found with living queens were assumed to have been killed in queen-to-queen combat. Spiders were assumed to have killed dead queens found in thorns occupied by spiders or bound by spider webbing, and dead queens found with other insects (moth larvae, beetle larvae, and occasionally ant workers) were assumed to have died because of the other insects present. Dead foundresses discovered without an indicator of probable cause of death were assigned a source of mortality of "unknown". Mortality data were pooled across both sites and years, and a chi-squared test was conducted to determine whether sources of mortality varied significantly among the three species.

To characterize patterns of parasitism across samples, we used maximum likelihood categorical analyses (the CATMOD procedure, SAS-Institute, 1992) to test the hypothesis that the frequency of parasitized claustral colonies is influenced by foundress species, sampling site, and sampling year. All three predictor variables were included in a single model, but we could not test for interactions within that 3-way model because *T. penzigi* foundresses were absent from one sample. We subsequently used a series of 2-way models to look for significant interaction terms, but the results of those analyses are reported only anecdotally here.

We used brood counts from our samples to estimate the reproductive losses imposed on young colonies by the parasitic wasp. Wasps we discovered were assigned to one of three developmental categories: 1) young larvae < 2 mm long; 2) late instar larvae ≥ 2 mm long, and 3) fully grown (pupae or adults, ca. 4.5 mm long). The total number of ant brood (eggs + larvae + pupae) was counted within each of these parasitized colonies. No colonies with detectable parasites had produced nanitic workers. In only two cases did we observe two *T. laikipiensis* within a single claustral colony, and those thorns were excluded from the analysis. To estimate the reproductive potential of an unparasitized queen, we counted the number of offspring produced by singleton foundresses of each species which met two criteria: 1) at least one ant pupa had been produced (indicating that significant time had elapsed since the queen colonized that thorn); and 2) if nanitic workers were present, the thorn was still tightly sealed (indicating that workers were not yet foraging outside the nest chamber). These criteria were used to exclude young claustral colonies which were still far from their maximum potential size. Within thorns meeting these criteria, we compared the effects of parasitism and pleometrosis on the success of *C. mimosae* foundresses (n = 219 swollen thorns). For pleometrotic groups, we divided the total number of ant offspring counted within a claustral colony by the number of living queens inside that thorn to estimate brood production per queen. One-way analyses of variance were used to test the null hypothesis that average per-capita fecundity was the same for singleton queens as for queens in pleometrotic groups. We performed separate tests for unparasitized colonies and for colonies in which we found late-stage larvae, pupae, or adults of *T. laikipiensis*. Finally, we used Fisher's exact test (Zar, 1996) to determine whether the probability of having any ant brood survive parasitism was different for single foundresses versus for pleometrotic groups. For all of these analyses, offspring counts for parasitized and unparasitized queens were pooled across both sites and years.

Results

Foundress queens are densely distributed on saplings of *A. drepanolobium* in our study sites (Table 1). Across all four samples (two sites in each of two years), in which we inspected the contents of 1216 occupiable swollen thorns, we discovered 1537 foundress queens, of which 72.1 % were alive at the time of collection. The frequencies of foundress queens of the three species differ dramatically and consistently between the two sampling sites. *C. mimosae* foundresses were most abundant at the Exclosure site (comprising 57.6 % and 48.9 % of all queens in 2001 and 2004, respectively), whereas *C. nigriceps* foundresses were nu-

merically dominant at the Mudhole site (accounting for 74.9 % and 94.8 % of all queens sampled in 2001 and 2004, respectively). *T. penzigi* queens accounted for 11–28 % of foundresses on saplings at the Exclosure site, but were very rare at Mudhole in both years.

Our surveys confirm the existence of strong exploitation competition among foundress queens searching for nesting sites. The percentage of available swollen thorns that were still uncolonized by foundress queens ranged from 1.1 % at Mudhole in 2004 to 16.1 % at the Exclosure site in that same year (Fig. 1). Similarly, the average number of foundresses (dead + alive) per available swollen thorn ranged from 1.67 to 1.22 in 2004 at the Exclosure and Mudhole sites, respectively. For all four samples, dead and alive foundress queens were significantly hyper-dispersed among available swollen
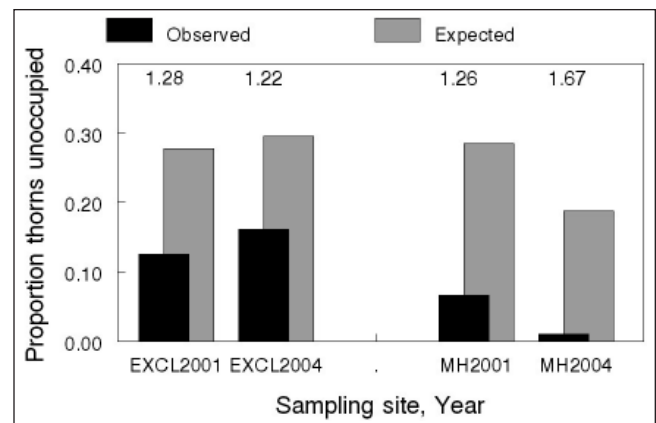

Figure 1. The proportion of swollen thorns on *A. drepanolobium* saplings that are empty and available for colonization by foundress queens, compared with the proportion expected under a random colonization hypothesis. For each sample, the mean number of foundress queens (alive and dead) per available swollen thorn is shown above the bar graph. This mean was used to calculate expected frequencies of empty thorns based on a Poisson distribution. Samples were collected in 2001 and 2004 from two sites, Exclosure (EXCL) and Mudhole (MH). Numbers of available swollen thorns in each sample are given in Table 1. Thorns were deemed "unavailable" for colonization if they were damaged, occupied by spiders or insect larvae, or were on saplings fully colonized by mature acacia-ant colonies.

Table 1. Foundress queens of three acacia-ant species found by sampling swollen thorns on small saplings of *A. drepanolobium* in two sites (Exclosure and Mudhole) in two years. Numbers in parentheses are the proportion of foundresses of each ant species found dead within claustral chambers. Only potentially occupiable swollen thorns are included in these totals.

Sample site year	Swollen thorns surveyed	*C. mimosae* foundresses		*C. nigriceps* foundresses		*T. penzigi* foundresses	
		alive	dead	alive	dead	alive	dead
Exclosure 2001	509	296	98	132	78	69	11
Exclosure 2004	255	104	45	56	12	57	31
Mudhole 2001	361	68	18	242	77	19	2
Mudhole 2004	91	7	1	81	64	0	0
All samples	1216	475	162 (.254)	511	231 (.311)	145	44 (.233)

thorns (all χ^2 values > 80; d.f. ranging 3–5; all P << 0.0001). Uncolonized swollen thorns were much rarer than expected (Fig. 1), and thorns with just a single queen were consistently more common than expected under a random colonization hypothesis (69.6% versus 35.4% expected, over all samples). Thorns containing more than a single foundress (including dead queens) were half as frequent as would be expected if queens were attempting colonizations independently of one another (19.7% versus 36.9% expected). These patterns indicate that foundresses try to avoid swollen thorns that are already occupied. Nonetheless, because suitable nest initiation sites are so limited, direct interference competition between prospective foundresses is also intense. These estimates of competition intensity are conservative, given that they include swollen thorns with pleometrotic foundresses of *C. mimosae*. In all, 15.6% of living *C. mimosae* foundresses were found in pleometrotic groups.

In interspecific contests between foundress queens attempting to colonize the same swollen thorn, we confirmed a strong hierarchy of fighting ability that was suggested in earlier surveys of young colonies at the Exclosure site (Stanton et al., 2002). Across all four samples, *T. penzigi* foundresses dominated in combat with *C. nigriceps* (23/23 contests won; P < 0.0001) and with *C. mimosae* (16/16 contests won; P < 0.0001). In 51 contests between *C. nigriceps* and *C. mimosae* foundresses, *C. nigriceps* survived 84.3% of the time (P < 0.0001). Based on these data, we conclude that *T. penzigi* foundresses have the greatest ability for interference competition with queens of other species, whereas *C. mimosae* foundresses perform the most poorly at this stage of colony establishment. Based on our "snapshot" sampling method, we could not determine whether pleometrotic groups of *C. mimosae* are better able to compete with singleton foundresses of *T. penzigi* or *C. nigriceps* during colony initiation.

Other prospective foundresses pose the greatest challenge to the survival of claustral colonies in this system. Pooled across all four samples, we attributed 79.1% of foundress deaths to combat between prospective queens. Spiders and insects living inside swollen thorns accounted for 10% of queen mortality, and less than 3% of claustral queen deaths could be attributed to attacks by ant workers. Chi-squared analysis demonstrated that foundresses of the three study species experience somewhat different sources of mortality (Fig. 2; χ^2 = 13.955; d.f. = 6; P = 0.0301). Eighty nine percent of foundress deaths in *T. penzigi* were attributed to fights with other queens, and in all 40 cases we discovered, the death was due to intra-specific combat. In contrast, combat with other queens accounted for 71% of deaths in *C. mimosae* (45.5% due to inter-specific fights), and these queens were more vulnerable to attack by spiders and insects living within swollen thorns. On average, we were unable to identify a likely cause of death in 4–12% of the dead foundresses discovered.

For foundress queens that survive to produce brood, parasitism by the wasp *T. laikipiensis* can pose a significant threat to success of the incipient colony, although rates of parasitism vary between sites and years, as well as among ant spe-
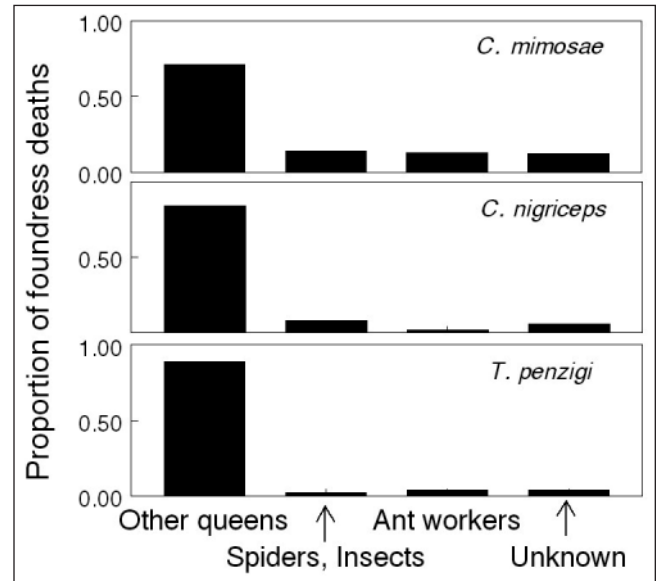

Figure 2. Apparent sources of mortality for claustral queens of three acacia-ant species. Data are pooled for all samples. Sample sizes are given in Table 1.

cies (Fig. 3). Rates of brood parasitism were high for claustral *C. nigriceps* colonies at the Mudhole site in 2001 (52/237 colonies parasitized = 21.9%) and 2004 (15/98 = 15.3%), where this species is most abundant (Table 1), but were usually less than 5% at the Exclosure site. Rates of brood parasitism were consistently high for *C. mimosae* in 2001 samples at the Exclosure site (46/263 colonies = 17.5% parasitism) and at the Mudhole site (15/98 colonies = 15.3% parasitism), but were very low in 2004 samples. In contrast, incipient colonies of *T. penzigi* were rarely parasitized by *T. laikipiensis* wasps (2/145 colonies had detectable brood parasites). Maximum likelihood analysis of parasitized and unparasitized colonies indicates that average rates of parasitism varied among foundress species (χ^2 = 11.77, 2 d.f., P = 0.0028), sites (χ^2 = 22.27, 1 d.f., P < 0.0001), and years (χ^2 = 14.57, 1 d.f., P < 0.0001). Two-way models usually revealed substantial interactions between pairs of these factors. Rates of parasitism on claustral colonies of *Crematogaster* can be high, but are highly variable spatially and temporally.

For claustral colonies with single queens, hosting a successful (mid- to late-instar) brood parasite is catastrophic. Colonies of *C. mimosae* and *C. nigriceps* in which early stage *T. laikipiensis* larvae were detected had 25–75% fewer brood than unparasitized colonies (Fig. 4). Parasites that successfully reach late instar, pupal, or adult stages consume virtually all of a foundress queen's brood. We observed no antagonistic behavior of queens towards the parasites at any stage of development. Parasitized foundresses with no surviving offspring were often seen protecting wasp pupae or recently eclosed wasp adults.

Pleometrotic cooperation between claustral foundresses of *C. mimosae* may reduce the risk of total failure due to brood parasitism by *T. laikipiensis*. Of 284 single-queen
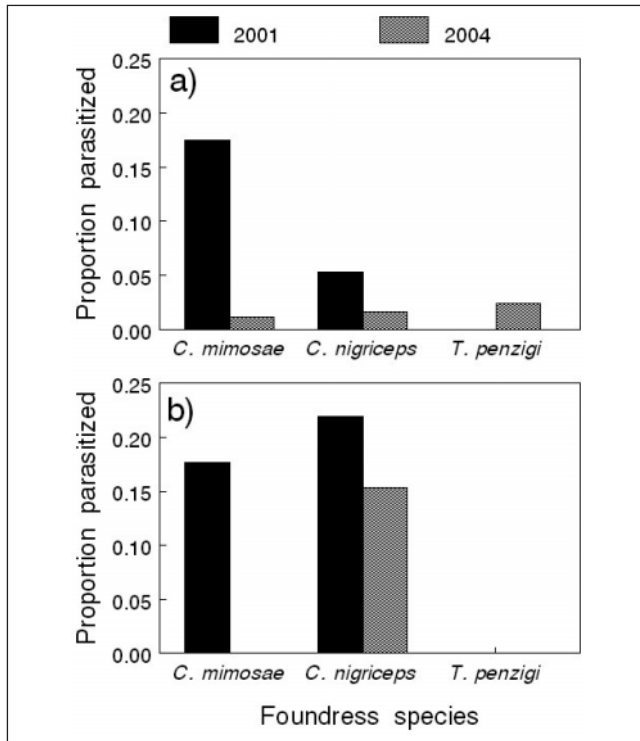
Figure 3. Proportion of claustral colonies of three acacia-ant species within which *Trigastrotheca laikipiensis* brood parasites were found. Data are presented for samples collected in 2001 and 2004 in two sites: a) Exclosure, and b) Mudhole. No claustral *T. penzigi* colonies, and only 7 claustral *C. mimosae* colonies, were found at the Mudhole site in 2004. Just 17 *T. penzigi* colonies were found at Mudhole in 2001. Remaining sample sizes range 58–263.
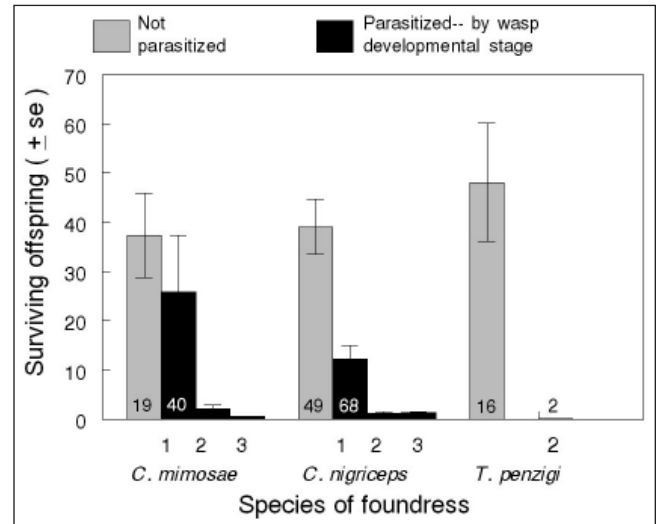

Figure 4. Impact of parasitism by the braconid wasp *T. laikipiensis* on brood production by claustral colonies of three acacia-ant species. All data are for colonies with single foundress queens. Maximum potential fecundity for colonies "not parasitized" was estimated by counting all brood in claustral colonies with pupae and/or young nanitic workers, but in which no wasp larvae or pupae were observed. Sample sizes for unparasitized colonies are shown in the grey bars. For claustral colonies with brood parasites, surviving brood were counted, and the developmental stage of the wasp was assigned to one of three categories: 1= early instar larva; 2= late instar larva; 3= pupa or adult. The number of parasitized colonies found for each species is shown. Data are from samples pooled across two sites and two years.

Discussion

Competition is frequently invoked as the principal ecological factor structuring ant communities (reviewed in Hölldobler and Wilson, 1990), but we know much more about competition between mature colonies than we do about competitive interactions early in colony establishment. Our data demonstrate that independent foundresses within a guild of East African acacia-ants experience intense exploitative competition, as they search for limited nesting sites, as well as mortal interference competition, as they fight over nesting sites they have discovered (also see Stanton et al., 2002). Studies of symbiotic plant-ants have consistently found that myrmecophyte saplings are colonized by multiple queens whose young colonies ultimately battle for exclusive possession of the host-plant (Janzen, 1975; Davidson et al., 1989; Longino, 1989; Perlman, 1992; Vasconcelos, 1993; Yu and Davidson, 1997; Yumoto and Maruhashi, 1999). Together, these observations indicate that competition among foundresses and among young colonies is an important factor shaping these communities.

Although the ecological role of parasites is less widely appreciated than that of competitors by ant ecologists, our data support the idea that parasites could have significant impacts on some ant communities. Negative effects of parasites on mature ant colonies are well known (also see Feener, 1981, 2000), but we have found only two previous studies of
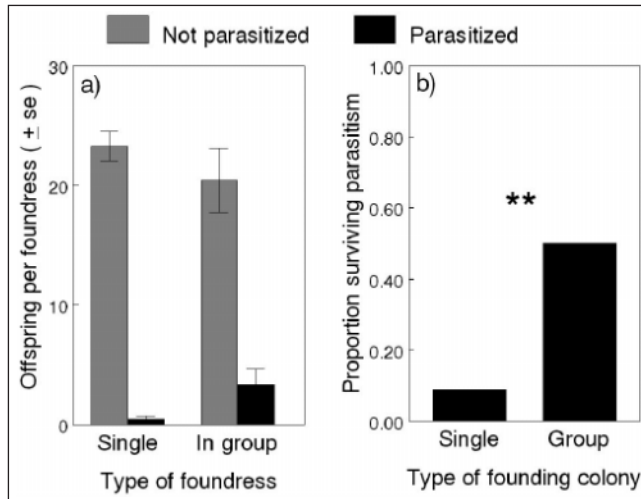
claustral *C. mimosae* colonies surveyed across both sites and years, 41 (14.4%) contained detectable parasitic wasps, whereas 21.9% of the 64 colonies with pleometrotic queens were parasitized. The effect of foundress group size on the incidence of brood parasitism is not statistically significant ($\chi^2 = 2.172$, 1 d.f., P = 0.1405), and the net result is that the ratio of wasp parasites to young queens was less for foundresses within cooperating groups (0.144 vs. 0.0745 for single and pleometrotic foundresses, respectively; $\chi^2 = 5.368$, 1 d.f., P = 0.0205). For claustral *C. mimosae* colonies without detectable wasp parasites, the average number of brood per foundress did not differ between single queens (23.27 ± 1.23 SE) and pleometrotic queens (20.45 ± 2.69 SE; ANOVA: F = 0.005; d.f. = 1, 181; P = 0.9437; Fig. 5a). Hosting a mid- to late-instar *T. laikipiensis* parasite dramatically reduced the mean number of offspring per foundress (Fig. 5a). Comparing the fecundity of parasitized singleton and pleometrotic foundresses by ANOVA was not possible because so many parasitized colonies produced no brood. However, parasitized colonies with multiple queens were significantly more likely to produce at least some brood than were parasitized colonies with single queens (Fig. 5b; Fisher's exact test: n = 44 colonies with mid- to late-instar brood parasites; P = 0.0092).

Figure 5. Consequences of parasitism for the reproductive success of singleton versus pleometrotic foundress queens of *C. mimosae*. a) Average number of offspring per queen in parasitized and unparasitized claustral colonies, comparing colonies with single queens to those with multiple queens. New foundresses that had not yet begun laying eggs were excluded from the totals for unparasitized colonies. b) The proportion of single-queen and pleometrotic colonies hosting late-stage wasp parasites in which at least some brood survived parasitism. Sample sizes follow: unparasitized single-queen colonies (154), parasitized single queen colonies (34), unparasitized pleometrotic colonies (29), parasitized pleometrotic colonies (12).

parasites attacking claustral queens. Gösswald (1950, cited in Hölldobler and Wilson, 1990) described a tachinid fly endoparasite of young ant queens that is cared for by workers after it emerges from the dead queen, and Yu and Quicke (1997) reported that up to 15% of *Azteca* foundress queens in domatia on *Cecropia* host-plants were killed by a braconid wasp ectoparasitoid. For the acacia-ants of *A. drepanolobium,* we found that rates of parasitism by the braconid wasp *T. laikipiensis* on claustral *C. mimosae* and *C. nigriceps* colonies could be locally high, whereas nearby colonies of *T. penzigi* were very rarely parasitized. We do not yet know whether this difference in attack rate between species reflects specialization by the wasp on *Crematogaster* or better defenses against the wasp in *Tetraponera*, but when parasites can destroy up to 20% of incipient colonies in some species, they have the potential to influence both patterns of selection within ant populations and the species composition of the ant community.

Why do species of foundress queen vary in their vulnerability to parasites and other intruders? We suspect that this has to do with both fighting ability and the thoroughness with which foundresses seal their entrance holes into the nesting chamber. *T. penzigi* dominates other species in queen-to-queen combat. Given that metabolic resources are very limited for claustral ant colonies (Keller, 1991; Tschinkel, 1993; Liu et al., 2001; Ode and Rissing, 2002), it is possible that *T. penzigi* foundresses maintain their fighting ability by reducing resource allocation to their initial brood (Tschinkel, 1993; Stanton et al., 2002). *T. penzigi* foundress-

es also make very strong entry-hole seals which may increase their resistance to attack by brood parasites, spiders, and thorn-dwelling insects. Accordingly, by far the greatest threat to claustral *T. penzigi* queens are other queens of the same species. Conversely, the relatively crude entry-hole seals made by claustral *Crematogaster* foundresses (especially *C. mimosae)* may make them more susceptible to parasitic wasps, and may also explain their greater vulnerability to attack by spiders and thorn-dwelling insects. Seals appear to be a vulnerability, as we have often observed later-arriving queens attacking the seal made by a previous foundress, rather than chewing through the wall of the swollen thorn itself.

Our data suggest that pleometrosis in *C. mimosae* may ameliorate the impacts of both parasitism and competition on colony establishment. High parasite loads could contribute to selection for pleometrotic colony founding in *C. mimosae*, since the per-capita risks associated with parasitism are less for cooperating foundresses (Fig. 5b). Because a group of cooperating foundresses produces greater numbers of workers (Fig. 5a), pleometrosis is also likely to increase a young colony's ability to compete with other young colonies for possession of host tree saplings. It is also possible that pleometrosis alters the competitive hierarchy among foundress queens fighting for nest initiation sites, but our data do not allow us to test this hypothesis.

In our samples, we found that very few claustral queens had been killed by workers from other ant colonies, but our data almost certainly underestimate the danger posed by established ant colonies to young queens. Colonies of all three *Crematogaster* species in this guild can occupy multiple trees, and will attempt to take over nearby saplings once they produce enough swollen thorns. We explicitly avoided sampling swollen thorns from saplings that were fully occupied by workers of mature colonies, as attacking workers usually remove the bodies of killed foundresses from thorns they invade. Once an active, mature colony moves workers and brood onto nearby saplings, those host-plants become unsuitable colonization targets for foundresses.

Given their relatively simple guild structure, identifiable resources, and strong ecological interactions, ant-myrmecophyte systems offer excellent opportunities for studying the dynamics of ant communities and for testing ecological theories (Heil and McKey, 2003; Palmer et al., 2003). Plant-ants are especially tractable for studies of the early stages of colony establishment (Perlman, 1992; Vasconcelos, 1993; Yu and Davidson, 1997; Baldacci and Tschinkel, 1999; Yumoto and Maruhashi, 1999; Stanton et al., 2002; Feldhaar et al., 2003; Nery and Vasconcelos, 2003), and so should provide us with many future insights into the roles of competition and parasitism in structuring these ant communities.

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