

Impacts of worker density in colony-level aggression, expansion, and survival of the acacia-ant *Crematogaster mimosae*

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Abstract. Experimental studies assessing the impact of demographic changes on aggression and inter-group competitive outcomes in communities of social species are rare. This gap in our knowledge is important, not only because social species are foundational elements of many terrestrial ecosystems, but because interference competition among social groups often involves decision-like processes influenced by demographic and environmental contexts. In East Africa, the symbiotic ant *Crematogaster mimosae* is a co-dominant competitor that engages in high-mortality, intra- and interspecific battles for sole possession of host trees. We manipulated worker density on *C. mimosae* Acacia host trees, and the colony's opportunity to expand onto neighboring trees to identify how these factors influenced colony-level aggression, expansion success, and longer-term survivorship. Worker density on focal trees was increased through translocation of domatia-bearing branches, and was decreased using partial tree fumigations. We examined impacts of density manipulations on aggression and immediate expansion success under two different risk scenarios. We tied focal trees to either an experimentally emptied-tree (low-risk treatment), or to a *C. nigriceps*-occupied tree (high-risk treatment). Expansion success onto emptied neighbor trees was 100% for controls and increased-density colonies, but only 50% for decreased-density colonies, despite the fact that host trees are a limiting resource in this system. Success expanding onto trees occupied by a heterospecific competitor reached 36%, 40%, and 79% in decreased, control, and increased-density trees, respectively. Our results show that changes in worker density due to disturbances or inter-group battles have the potential to disrupt competitive hierarchies. Worker density manipulations also affected longer-term colony persistence. Behavioral and genetic data revealed that 12 months after expansions 100% of the decreased-density colonies, and 25% of control and increased-density colonies, had been supplanted by neighboring opportunistic conspecifics. Intraspecific aggression may have lower costs in *C. mimosae* because aggressive colonies can incorporate workers or queens from defeated competitors. The unexpectedly high frequency of conflicts between conspecific *C. mimosae*, in combination with behaviors decreasing the cost of intraspecific competition relative to interspecific conflict, may create opportunities for the survival of subordinate competitors in this ant–plant system.

Key words: Acacia drepanolobium; aggression; coexistence; *Crematogaster mimosae*; density; interspecific competition; intraspecific competition; mutualism; myrmecophyte.

INTRODUCTION

Understanding how competitors interact and coexist is a major focus for ecologists. Both empirical and theoretical evidence suggest that coexistence among competitors is more likely under stronger intraspecific than interspecific competition (Yang et al. 2010, Fujiwara et al. 2011, Barabás et al. 2016). There is substantial consensus that the frequency and intensity of intra- and interspecific interactions are influenced by the relative abundances and spatial distributions of species within the community (Mumby and Wabnitz 2002, Bascompte and Jordano 2007, Maire et al. 2012, Martorell and Freckleton

2014), but little is known about how population dynamics mediate antagonistic interference interactions among social competitors (but see Hou et al. 2010, Cubaynes et al. 2014).

Interference competition occurs when a dominant competitor prevents or displaces others from accessing a limited resource, and in animal species often involves within and between-species aggressive interactions (Amarasekare 2002, 2003). The level of aggression displayed by competitors during such interactions is influenced by the potential benefits obtained by winning a contest, and the risks faced during confrontations (Maynard-Smith 1982, Enquist and Leimar 1987, Innocent et al. 2011). Accordingly, fluctuations in resource availability, competitive ability, or changes in the population density of competitors are likely to

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influence the coexistence of antagonistic competitors (Brown 1989, Sih et al. 2012, Flynn and Pereira 2013, Jiang et al. 2015).

In communities of social species, antagonistic interference competition is common and a variety of mechanisms modulating coexistence among social species have been proposed (Savolainen and Vepsäläinen 1988, Gotelli 1997, Houle et al. 2006). For example, in many social species, group demographics (London and Jeanne 2003, Grover et al. 2007), or individual and collective personalities (Courchamp et al. 2002, Pruitt et al. 2013, Jandt et al. 2014, Keiser and Pruitt 2014) impact short-term cooperation and competitive success. Group size in particular is a critical determinant of competitive success among social species, with larger groups often dominating during territorial confrontations (Adams 1990, Palmer 2004, Tanner 2006, Mosser and Packer 2009). Moreover, larger groups require higher quality and quantity of resources to sustain natural population dynamics, and therefore the ability of a group to successfully defend or further expand its territory is expected to fluctuate with group size and the cooperative dynamics operating within the group (Balshine et al. 2001, Campbell et al. 2005, Lopez-Sepulcre and Kokko 2005). In social insects, some evidence exists that fluctuations in resource availability and demographics can impact cooperative behaviors (e.g., Haridas and Rajarshi 2001, Lehmann et al. 2006, Sorvari et al. 2014) and, in Argentine ants, variations in food nutritional value can modify competitive behaviors and success (Kay et al. 2010). Nevertheless, studies examining effects of resource and demographic stochasticity in modulating aggression and competitive success among social groups have largely been focused in mammals (Ember and Ember 1992, Aureli and De Waal 1997, Moore 1999, Koenig 2002, Harris 2010, Mitani et al. 2010, Stockley and Bro-Jørgensen 2011, Cubaynes et al. 2014). These studies show that intergroup antagonistic confrontations can have immediate fitness costs (energy loss, injury, or mortality), and benefits (enhanced access to food or mates) for the participants (Kitchen and Beehner 2007, Crofoot 2013, Georgiev et al. 2013). Recent work on social birds and monkeys has revealed that inter-group aggression can also have lasting consequences for reproductive success, social status, and vulnerability (Stockley and Bro-Jørgensen 2011), or modify social bonding and longer-term decision making (see Radford and Fawcett 2014). However, longer-term consequences of inter-group conflict in eusocial insect communities have not been investigated, despite the fact that they are among the most abundant organisms in terrestrial ecosystems (Wilson 1990, Holldobler and Wilson 2008), and have been widely utilized to examine biotic interactions and community structuring (e.g., Palmer et al. 2003, Bascompte 2009, Amarasekare 2015).

Despite the prevalence of inter-group interference competition among social species, experimental manipulations to examine impacts of group density on aggression, competitive success, and longer-term persistence appear

to be lacking. To fill this gap, we conducted experiments in East Africa on a keystone ant–plant mutualism: *Acacia drepanolobium* and its guild of symbiotic ants (Madden and Young 1992). In this myrmecophyte, four symbiotic ants compete aggressively for sole possession of host trees against intra- and interspecific neighbors (Young et al. 1997). Trees provide nesting space and food, but available mature trees are rare (>98% of trees are occupied), leading to territorial confrontations that result in high mortality (Palmer 2004). Previous work on this system revealed that despite the existence of an average linear competitive hierarchy correlated to colony size, competitors are able to coexist at local scales (Palmer 2004). Siepielski et al. (2010) recently suggested that true coexistence can only arise when rare species are able to increase despite all other competitors being present at normal abundances (invasibility criterion). In the *A. drepanolobium* ant–plant system, subordinated species resort to specialized behaviors that reduce niche overlap (Stanton et al. 1999, Palmer et al. 2002). These behavioral adaptations increase subordinate survival and growth by reducing competitive encounters, and thus are likely to contribute to the fulfilment of the invasibility criterion sensu Siepielski et al. (2010). Although deterministic explanations such as the evolution of priority effects help us understand the coexistence in this system, the relative contribution of stochastic events such as demographic fluctuations may have in promoting or disrupting species coexistence remains unknown in this and most myrmecophytes. To examine whether fluctuations in colony demographics affected short-term and longer-term competitive dynamics among the symbiotic competitors on this system, we designed an experiment to establish causal links between sudden changes in ant density, intergroup aggression, and the short- and longer-term colony persistence after territorial expansions.

First, we modified worker density in trees of the co-dominant ant species *Crematogaster mimosae*, and examined how demographic perturbations impacted short-term colony-level aggression and competitive success. In addition, we manipulated the potential mortality costs of territorial expansion by offering experimental colonies the opportunity to expand either onto an emptied neighboring tree (a low-risk, no-mortality scenario) or by aggression onto a tree occupied by a colony of *C. nigriceps* (a higher-risk, high-mortality scenario). The combination of our two manipulation levels allowed us to examine whether expansionist colony-level behaviors reflect immediate or perceived long-term risks and benefits. To the best of our knowledge, no other study in social insects has examined the consequences of colony expansion beyond the immediate opportunity to secure limited resources. Our study is also novel because we use molecular markers to measure intraspecific competition rates within a dominant competitor, and discuss its potential importance for the long term competitive coexistence on this keystone ant–plant mutualism. We specifically tested the following short-term and longer-term hypotheses.

*Short-term effects on aggressive engagement
and expansion*

H₁.—In most social species, larger groups exhibit greater aggression and win most territorial confrontations (Adams 1990, Palmer 2004, Tanner 2006, Hardy et al. 2013). We thus expect *C. mimosae* colonies with increased density to exhibit higher levels of aggression and greater expansion success against heterospecific competitors than control and decreased-density colonies.

H₂.—For two reasons, we expect increased-density colonies to be more successful in expanding onto emptied-trees than control and decreased-density colonies. First, because territorial expansions further reduce density, and are thus likely to exacerbate colony vulnerability to takeovers. Second, because larger groups are often more efficient in detecting, utilizing, and defending resources (Grover et al. 2007, Donaldson-Matasci et al. 2013), and therefore more likely to sense and rapidly colonize newly available trees.

Longer-term colony vulnerability and expansion costs

H₃.—Larger territories require more individuals to be successfully defended, and larger groups are often more aggressive and win most confrontations (Tschinkel et al. 1995, Adams 2001). Therefore, we expect colonies with experimentally increased densities to survive better post-expansion periods of critical vulnerability, and retain newly acquired territories for longer compared to the un-manipulated and decreased-density colonies.

H₄.—Inter-colony battles over host trees result in high worker mortality that may increase colony vulnerability (Rudolph and McEntee 2015). We therefore expect colonies that expanded through defeating occupied trees to subsequently be less successful in retaining territory than those that expanded onto emptied trees without suffering mortality.

METHODS

Study site and system

Our study was conducted at the Mpala Research Centre (0°17' N, 37°52' E, 1800 m) on the Laikipia Plateau in Kenya (Ruiz Guajardo et al. 2010). The area is predominantly semiarid grassland savanna dominated by *Acacia* (*sensu lato*) and *Commiphora* trees, has a weakly tri-modal rainfall pattern (550–600 mm), and a dry season spanning December to March (Ruiz-Guajardo 2008, Baldock et al. 2011). The myrmecophyte tree *Acacia drepanolobium* is a dominant species (>98%) across areas characterized by “black cotton” vertisol soils (Young et al. 1997). In this ant–plant system, individual trees host one of four mutually exclusive symbiotic ants (*Crematogaster sjostedti*, *C. mimosae*, *C. nigriceps*, *Tetraponera penzigi*), which defend their trees against herbivores in exchange

for nectar and shelter (Madden and Young 1992, Young et al. 1997). Ant colonies engage in intensive intra- and interspecific conflicts for sole possession of trees in which thousands of workers may perish (Young et al. 1997, Palmer et al. 2000). Within the local study area, the two most common species are *C. mimosae* and *C. nigriceps* (Young et al. 1997), and interspecific battles between them are common, making them an excellent choice for examining interference competition dynamics.

Initial colony characterization

In October 2012, using aggression assays we identified and genetically characterized 60 *C. mimosae* individual colonies, each occupying two or three 1.5–2.5 m trees that were adjacent to a *C. nigriceps* colony (see Appendix S1A–D). We selected one “focal tree” for each ant species, matching for height, stem diameter, and ant activity. To track the future expansion or contraction of experimental *C. mimosae* colonies, we collected 50 workers from each tree, preserving them in 99% ethanol for DNA microsatellite analyses.

We characterized patrolling ant density on focal *C. mimosae* trees by kicking the trunk five times, and counting the number of ants patrolling three 30-cm trunk lengths for 30 s following the disturbance. To minimize effects of temperature variation on colony activity levels, patrolling density surveys were conducted between 09:00 and 12:00 on sunny days only. Post-disturbance patrolling worker density is significantly and positively correlated with the estimated total number of workers on the tree (see Appendix S2: Fig. S1); thus, patrolling worker density is a reasonable proxy for total worker density.

We estimated group aggression level on focal *C. mimosae* trees as the “time to fight” after a heterospecific encounter. We vigorously kicked the tree main stem five times, placed an opened swollen thorn (domatia) containing workers from a nearby *C. nigriceps* tree onto a branch with ≥ 5 *C. mimosae* workers patrolling, and measured the time elapsed until a fight ensued. To ensure that our measurements reflected aggression and not encounter rates, we did not start recording time until after *C. mimosae* individuals had encountered *C. nigriceps* intruders. We started the clock when at least two pairs of heterospecifics were observed displaying aggressive behaviors such as rapid antennation, opening and closing of jaws, and quick movement of the gasters, and stopped recording time when two or more individuals were observed biting legs or heads.

Experimental density manipulations

We randomly assigned 20 experimental *C. mimosae* colonies to each of three density treatments: decreased density, control, and increased density. In control colonies, we did not alter the number of domatia or workers. In decreased-density colonies, we reduced worker numbers by wrapping 50% of domatia on each tree in a plastic sheet, and spraying each of them with a

pyrethroid insecticide (Bestox® α -cypermethrin, FMC Corporation, Philadelphia, USA). This insecticide is highly toxic to arthropods, minimally toxic to vertebrates, and degrades rapidly. To increase the number of workers, we translocated cut branches from non-focal trees in the same colony, and attached them to the focal tree using galvanized wire, until a 50% increase in domatia number was achieved (e.g., if the focal tree had a total of 50 domatia, we translocated branches until 25 domatia have been added). To prevent ants from migrating away from focal trees, we applied Tanglefoot barriere (Tanglefoot Company, USA) to the main stems of all focal trees in the increased-density treatment. Because *C. mimosae* forages for insect prey on the ground, the sticky barrier was allowed to degrade over the next two weeks.

Analyses of density effects on colony-level aggression

Four weeks after manipulating density, we remeasured patrolling ant density and time to fight for each experimental *C. mimosae* colony, allowing us to compare pre- and post-treatment densities and aggression levels. We used ANOVA to test for significant variation among manipulation treatments, with change in the number of patrolling ants as the response variable (post-treatment minus pre-treatment patrolling density), and density treatment as a fixed factor. We used ANCOVA to assess whether experimental changes in the number of workers affected group aggression levels, with time to fight as the response variable, density treatment as a fixed factor, and post-treatment patrolling ant density as a covariate. These and all subsequent analyses were performed using the GLM function in R 3.1.0 core stats package (R Core Team 2014). Data used in all models met assumptions for normality and homogeneity of variance.

Expansion opportunity and aggression

Six weeks after establishing ant density treatments, we gave one-half of the focal *C. mimosae* trees within each density treatment the opportunity to expand onto an experimentally emptied neighbor tree or an occupied *C. nigriceps* tree. A portion of the focal *C. mimosae* tree was tied to the neighbor, creating a fully factorial (3×2) design in which density treatment (decreased, control, increased) is crossed with expansion type (emptied vs. occupied-neighbor), with 10 colony pairs allocated to each treatment combination. Experimentally emptied trees were created by exterminating all *C. nigriceps* ants using Bestox, and applying Tanglefoot to the base of the tree to prevent recolonization. To prevent degradation of the density treatments by recruitment of *C. mimosae* workers from non-focal trees onto the focal joined trees, we applied Tanglefoot to all control and increased-density trees and maintained the barrier until there was a clear expansion outcome. No Tanglefoot was applied to decreased-density non-focal trees, because worker numbers had been reduced across the entire colony.

Upon tying together each focal pair of *C. mimosae* and occupied *C. nigriceps* trees, we measured two additional components of heterospecific aggression. We recorded “time to warfront formation” as the time elapsed from the moment the trees were tied together until multiple heterospecific individual fights occurred within the contact zone. “Time to invade” was recorded when *C. mimosae* workers moved beyond the contact zone and began raiding broods from the *C. nigriceps* domatia. To assess whether *C. mimosae* worker density affected aggression during expansion events, we used ANCOVA, with log-transformed time to warfront formation or time to invade as responses, and density treatment and post-treatment patrolling density as fixed covariates.

Because confrontations with occupied neighbors resulted in a winner within a few days, after one week, we scored the outcome as either “*C. mimosae* expansion” or “*C. mimosae* no expansion.” In the latter case, *C. nigriceps* had defeated and exterminated *C. mimosae* on its focal tree. In the emptied neighbor treatment, colonies expanded over a period of several weeks, and therefore a “*C. mimosae* expansion” was only recorded if, after 3 months, at least 20% of the domatia on the emptied tree had been colonized; otherwise, we recorded the result as “no expansion.”

Longer-term cost of expansion and vulnerability

To determine the longer-term fate of experimental *C. mimosae* colonies that survived expansion tests, we resurveyed focal trees and all nearby trees 12 months after initiating density manipulations. We recorded ant species identity and colony boundaries, and examined how different treatments affected post-expansion inter- and intraspecific takeover rates of focal and non-focal trees within the original colony. If the ant symbiont was no longer *C. mimosae*, that tree was scored as an interspecific takeover against the original experimental colony. We remapped colony boundaries on trees still occupied by *C. mimosae* using behavioral aggression assays. Later genetic fingerprinting was used to determine which *C. mimosae*-occupied trees (1) were still occupied by the original experimental colony, (2) were new trees not originally part of the colony but now occupied by the same ant colony (expansions of experimental colony), or (3) had been taken over by neighboring conspecifics (see Appendix S1A–D).

Logistic regression

We used logistic regressions to examine whether density treatment and neighbor type significantly affected short-term focal expansion success, and the longer-term fates of focal and non-focal trees within experimental *C. mimosae* colonies. Analyses of focal trees incorporated all three density treatments, but because no experimental increases of density were performed in non-focal trees, this treatment was excluded from longer-term analyses of the fate of non-focal trees. To control statistically for natural variation in density among experimental colonies, we included pre-treatment

patrolling density in all models assessing short-term expansion success. To examine longer-term consequences of expansion we used survivorship data from surveys performed 12 months after expansion events. We controlled for the effect of density manipulations by including post-treatment patrolling density as a covariate in the models. To determine whether the fate of the focal trees in the experimental colonies affected the survivorship of non-focal trees, we included initial focal expansion success in analyses of non-focal tree takeovers.

We show general patterns of expansion success and longer-term post-expansion survivorship using bar charts illustrating proportional success for each density treatment (decreased, control, increased) and neighbor type (empty or occupied). We describe probability of success for each factor level, referencing the corresponding figure and panel that best illustrates this pattern. We use odds ratios to statistically compare relative differences between levels within a factor. However, odds ratios are difficult to describe and to avoid unnecessary confusions, we follow the recommendations provided by Osborne (2006) and deliberately avoid lengthy descriptions of magnitudes and directions. Nevertheless, to confer how strong differences between groups were, we provide odds ratios and their statistical significance inside brackets (e.g., odds ratio = 5, $P = 0.05$). Odds ratios are less daunting when considering that values of 1 denote no difference between groups, and that the higher the number, the stronger the difference was between the groups compared. We are careful to clarify the direction of every comparison made, and Table 1 provides a summary of these.

TABLE 1. Logistic regressions to assess (A) focal tree short-term expansion success, (B) focal tree longer-term risk of takeover by opportunistic competitors, and (C) non-focal tree resident long-term fate.

| Response variable | β | z | Odds ratio | P |
|---|--------------|-------|----------------------|-------|
| A) Initial expansion success | | | | |
| Intercept | -1.62 (0.99) | -1.63 | | 0.102 |
| Control:decreased | 1.27 (0.73) | -1.79 | 3.58 (0.88–16.9) | 0.070 |
| Increased:control | 1.67 (0.91) | 1.84 | 5.30 (0.97–36.8) | 0.053 |
| Increased:decreased | 3.08 (0.94) | 3.28 | 21.77 (4.01–168.5) | 0.001 |
| Pre-treatment patrolling density manipulation | 0.07 (0.03) | 2.19 | | 0.028 |
| Neighbor empty:occupied | 2.57 (0.86) | 2.49 | 5.86 (1.58–26.8) | 0.012 |
| B) Focal takeover risk after 12 months | | | | |
| Intercept | -2.09 (1.96) | -1.50 | | 0.390 |
| Control:decreased | 4.15 (1.50) | 2.76 | 63.68 (5.40–2,675.5) | 0.005 |
| Increased:control | 0.23 (1.09) | 0.22 | 1.27 (0.14–12.6) | 0.826 |
| Increased:decreased | 4.39 (1.82) | 2.98 | 80.93 (6.85–3,256.8) | 0.003 |
| Post-treatment patrolling density | -0.03 (0.04) | -0.75 | | 0.454 |
| Neighbor empty:occupied | 1.69 (1.18) | 1.43 | 5.41 (0.69–113.9) | 0.153 |
| C) Non-focal takeover risk after 12 months | | | | |
| Intercept | -1.47 (0.71) | -1.95 | | 0.038 |
| Control:decreased | 2.91 (0.90) | 3.21 | 18.50 (3.57–133.8) | 0.001 |
| Neighbor empty:occupied | 1.51 (0.85) | 1.76 | 4.54 (0.90–27.9) | 0.077 |
| Focal expanded successfully | 0.22 (0.70) | -0.96 | 1.29 (0.30–5.1) | 0.754 |

Notes: For each model, we show response variables in boldface type, β coefficients (effect sizes) with standard errors in parentheses, P values, z values, and odds ratios with 95% confidence intervals in parentheses. Odds ratios for multilevel factors were computed using the direction of comparisons indicated in the first column, 95% CI that do not include 1 denote significant differences between groups. Density treatment was fitted as a fixed factor with three levels (models A, B), or two levels (model C), Neighbor type as a fixed factor with two levels, pre-treatment patrolling density (model A), and post-treatment patrolling density (model B) as continuous fixed variables. Focal expanded (model C) was fitted as a fixed factor with two levels. Odds ratios were not computed for continuous variables, because these only make sense when the likelihood of different outcomes is compared.

Molecular markers and analyses

For every experimental tree, we extracted DNA from 30 individuals and genotyped them using 15 highly polymorphic microsatellites. Of these, 10 markers had previously been developed (Rubin et al. 2009) and seven were newly designed for this study. We used COANCESTRY 1.0.1.2 (Wang 2011) to estimate within-colony genetic relatedness based on 15 workers collected at the beginning of the experiment (pre-treatment sample) and 15 collected 12 months after that (post-treatment). We then estimated relatedness among workers after combining both samples, and assessed whether mean relatedness dropped significantly, indicating that the pre- and post-treatment samples represented different *C. mimosae* colonies. We corroborated our results using COLONY v2.0.5.0 (Jones and Wang 2009) by identifying genetic sibships for pre- and post-treatment samples independently and combined. If none of the full-sib or half-sib groups showed mixed composition (containing individuals from both pre- and post-treatment samples), we inferred the samples to be from different *C. mimosae* colonies. A detailed description of the molecular protocols, PCR parameters, and the characterization of the seven newly developed markers is provided in the (Appendix S1B, C).

RESULTS

In comparison to control colonies, whose patrolling densities did not change over the course of the experiment, decreased-density colonies had on average 22

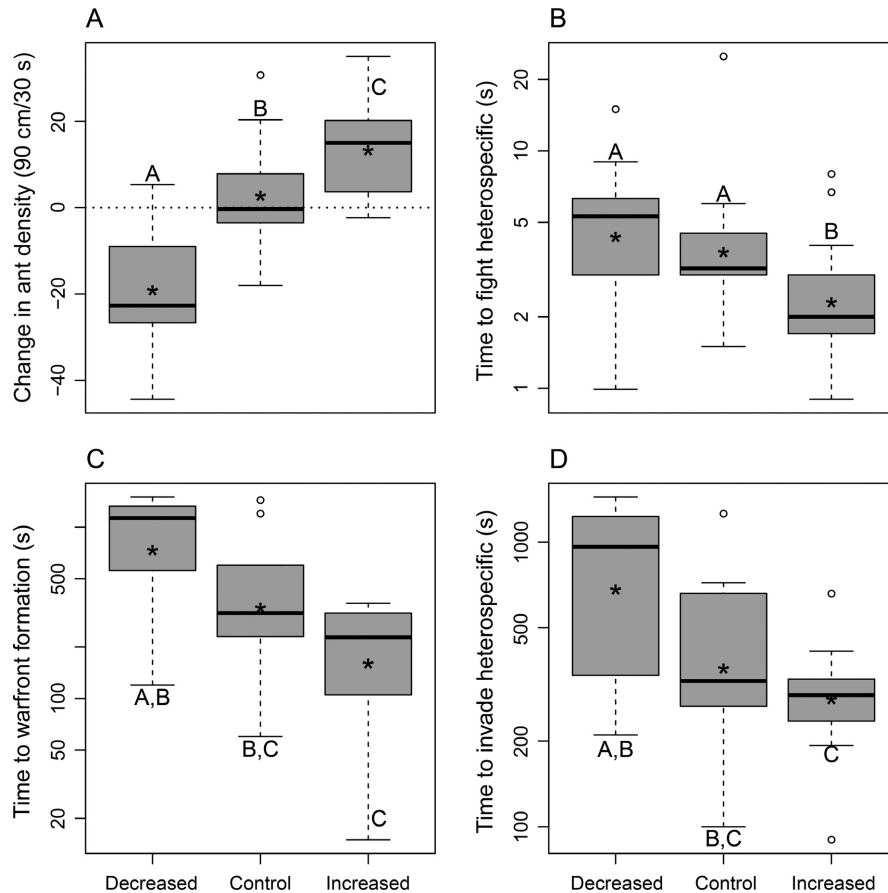


FIG. 1. Effects of *Crematogaster mimosae* worker density manipulations on four response variables. (A) Change in ant density on focal trees, comparing before- with after-treatment values. (B) Time to fight after encountering an introduced *C. nigriceps* ant. (C) Time to war-front formation after joining of host canopies occupied by heterospecific colonies. (D) Time elapsed after joining canopies until *C. mimosae* ants started raiding brood and larvae located in domatia of the experimentally joined *C. nigriceps*-occupied neighbor. Experimental *C. mimosae* colonies that lost confrontations or did not invade heterospecific trees after 25 min of observation were excluded from the analyses (panels C and D). The whiskers above and below the box plots indicate 95% confidence intervals (CI) around the means. Letters above or below whiskers represent significant differences in a posteriori Tukey contrasts applied to analyses summarized in Appendix S1: Table S1. The dots outside the 95% CI represent colonies with largely skewed values.

fewer ants ($P = 0.001$), and increased-density colonies 10.5 more ants per branch per scan (ANOVA, $F_{2,57} = 41.74$, $P = 0.048$, Fig. 1A; Appendix S2: Table S1A).

Short-term effects of density on aggressive engagement

Manipulations of worker density significantly affected colony-level aggression metrics and success in staged heterospecific conflicts (Fig. 1B–D). Increases in worker density resulted in more aggressive colonies, which as predicted (H_1), were also more successful during competitive confrontations against *C. nigriceps* (Fig. 1B–D; Appendix S2: Table S1B–D). Relative to the control, the mean time elapsed between initial contact and a full fight with heterospecific intruders was 0.52 s slower in the decreased-density treatment ($P = 0.63$), and 2.02 s faster in the increased-density treatment (ANCOVA, $F_{2,56} = 7.62$, $P = 0.045$, Fig. 1B; Appendix S2: Table S1B). Mean differences in the time to warfront formation (Fig. 1C),

and the time to invade (Fig. 1D) were not significant between the control and either density manipulation treatment. However, decreased-density colonies on average formed a warfront 723 s more slowly than did increased-density colonies (ANCOVA, $F_{2,31} = 9.72$, $P = 0.001$), and were also 533 s slower to invade occupied *C. nigriceps* trees (ANCOVA, $F_{2,27} = 5.08$, $P = 0.012$, Fig. 1C, D; Appendix S2: Table S1C, D).

Short-term effects of density on expansion success

The odds ratio and significance values reported in this and the following sections come from logistic regression analyses, whose summaries are presented in Table 1. After statistically controlling for neighbor treatment and for pre-treatment variation in ant density, we observed differences in short-term expansion success between the control and each density treatment that were large in magnitude but not statistically significant (control vs.

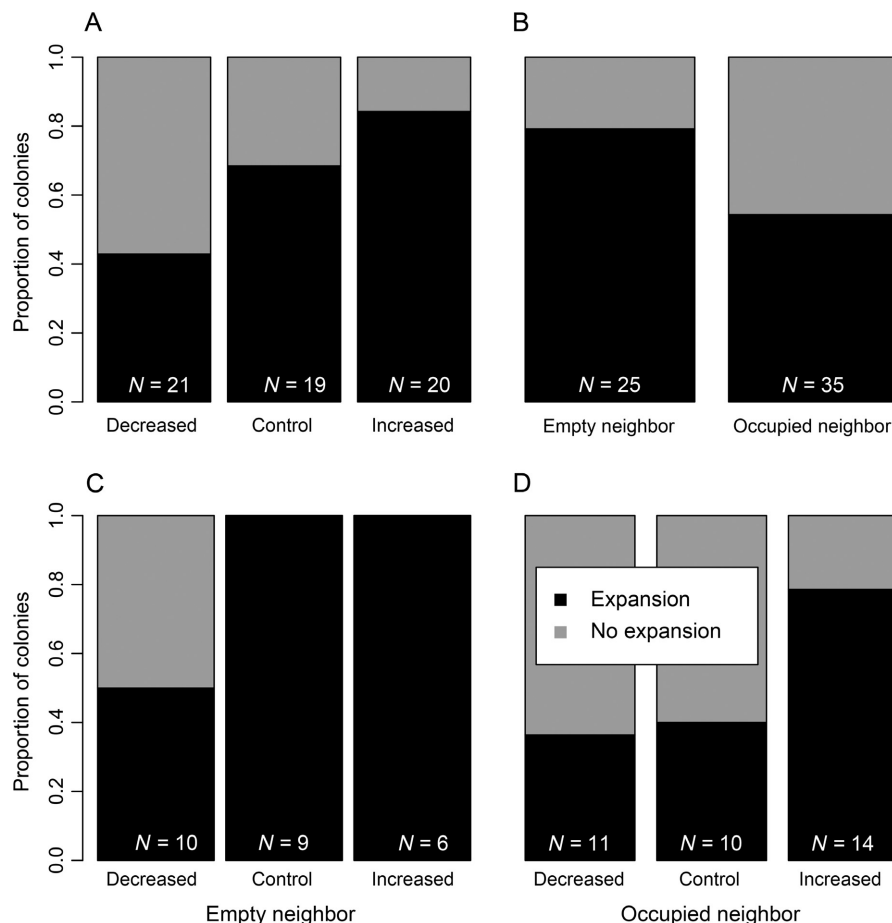


FIG. 2. Initial expansion success by focal *Crematogaster mimosae* trees subjected to two worker density manipulations and subsequently joined to either an experimentally emptied neighbor tree or a tree occupied by *C. nigriceps*. (A) Proportion of successful expansions as a function of density treatment. (B) Proportion of successful expansions as a function of neighbor treatment. (C–D) Proportion of focal trees split by density treatment that successfully expanded onto either (C) experimentally emptied neighbor trees or (D) heterospecific-occupied neighbors. In the occupied neighbor treatment, “expansion” represents the proportion of *C. mimosae* focal trees that defeated and survived the enforced confrontation with *C. nigriceps*. In the empty neighbor treatment, “expansion” represents the proportion of experimental colonies that had occupied at least 20% of the experimentally emptied tree 3 months after the canopies were joined. Statistical analyses of expansion success are summarized in Table 1A.

decreased, $P = 0.07$, control vs. increased $P = 0.053$, Table 1A, Fig. 2A). However, across both neighbor types, increased-density colonies were significantly more successful in expanding compared to the decreased-density treatment (odds ratio = 22, $P = 0.001$, Table 1A). The probability of successful expansion was 0.36 for decreased-density, 0.41 for control, and 0.78 for increased-density colonies (Fig. 2D).

We found strong support for the prediction (H_2) that colonies would be more successful expanding onto emptied trees than onto occupied trees (odds ratio = 6, $P = 0.012$, Table 1A). Across density treatments, the probability of successfully expanding onto an emptied tree was 0.80 and onto an occupied tree was 0.54 (Fig. 2B). Further, expansion success markedly differed among density treatments, with successful expansions onto emptied trees reaching 100% in the control and increased-density treatments and 50% in the decreased-density (Fig. 2C). In turn,

expansion success onto occupied trees was lower, reaching 36% for decreased-density, 40% for control, and 79% for increased-density colonies (Fig. 3D). All 13 *C. mimosae* colonies that failed to defeat occupied-neighbor trees were completely extirpated by the resident *C. nigriceps*.

Longer-term costs of expansion and vulnerability

Survivorship patterns 12 months after expansions supported our prediction (H_3) that higher densities would enhance longer-term tree defensibility and survival (Fig. 3A–D). While no significant differences in survivorship were observed between the increased-density and the control treatment ($P = 0.826$, Table 1B), decreased-density colonies did experience significantly higher mortality rates than did the control ($P = 0.005$) and the increased-density colonies ($P = 0.003$, Table 1B, Fig. 3A). Regardless of neighbor type, 12 months after expanding,

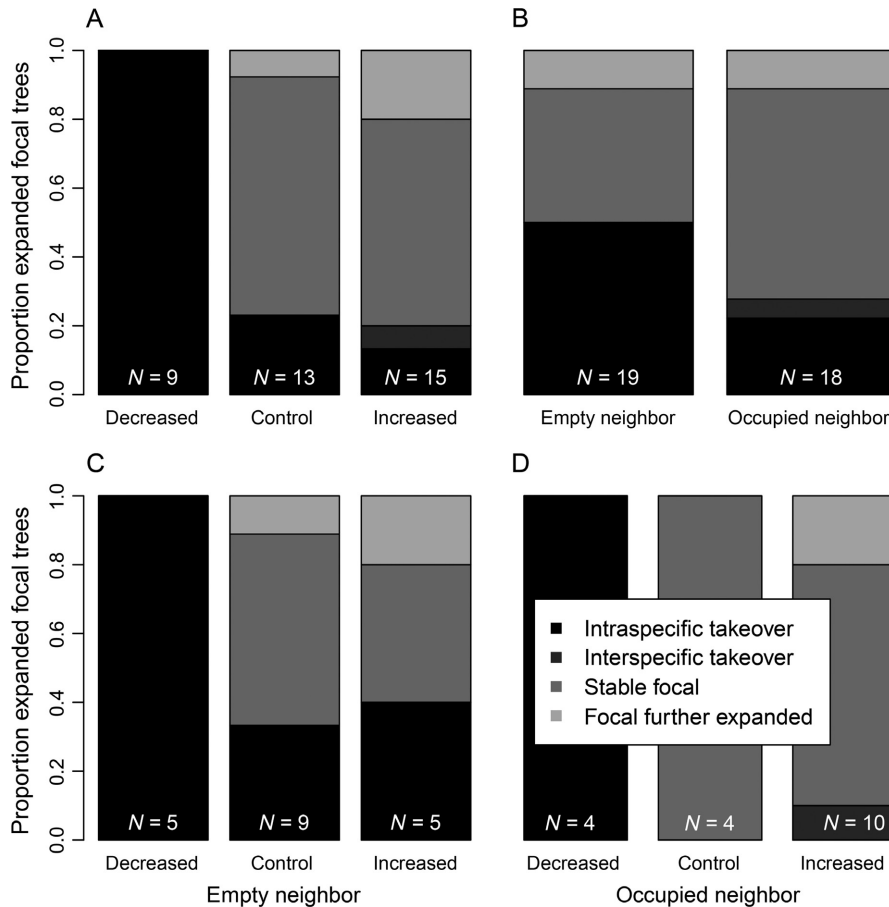


FIG. 3. Proportion of *Crematogaster mimosae* experimental focal trees, 12 months after initial expansion, that were stable (still inhabited by the original colony), had further expanded (inhabited by original colony but now also occupying trees originally not part of the experimental colony), or were taken over by an intraspecific or interspecific opportunistic neighbor. (A) Focal tree fate as a function of density treatment. (B) Focal tree fate as a function of neighbor treatment. (C, D) Focal tree fate, split by density treatment, for focal trees that expanded onto either (C) experimentally emptied trees, or (D) heterospecific-occupied neighbors. Sample sizes reflect the number of initial focal colonies that did expand onto neighbor trees when canopies were joined. Since only one *C. mimosae* focal tree was subsequently taken over by an opportunistic *C. nigriceps*, takeovers by heterospecifics and conspecifics were lumped together in logistic regressions to assess focal survival success (Table 1B).

all colonies in the decreased-density treatment had been extirpated from their focal trees. In contrast, within the same period of time 77% of the focal control trees (odds ratio = 64, $P = 0.005$, Table 1B), and 80% of the increased-density focal trees were still inhabited by the original experimental *C. mimosae* colony (odds ratio = 80, $P = 0.003$, Table 1B, Fig. 3A–D).

Contrary to our expectations (H_4), mortality costs incurred during successful confrontations with *C. nigriceps* did not increase the subsequent risk of takeover by opportunistic competitors (Fig. 3B–D). The probability of being killed by an opportunistic competitor after colonizing an emptied tree was 0.47, and after defeating an occupied tree was 0.27 (Fig. 3B). Further, a tendency for higher worker density to reduce subsequent risk of takeover was observed (Fig. 3C, D), but due to small sample sizes the interaction between neighbor type and density was not significant ($N < 10$, $P = 0.098$). Moreover, sample sizes were small ($N = 5$) but expansion at reduced

worker densities appeared to hold longer-term costs even when this occurred without a confrontation (Fig. 3C). Regardless of neighbor type, within 12 months of occupying new territories, all 10 reduced-density focal trees that had expanded had been killed by opportunistic competitors (Fig. 3C, D). In contrast, all five decreased-density focal trees that did not initially expand onto emptied neighbors still retained the original *C. mimosae* colony. Over the course of the experiment, three of those colonies eventually expanded onto the emptied experimental neighbor.

Evidence of intraspecific competition

Our combined behavioral and genetic assays revealed that, across density treatments, interspecific takeovers of *C. mimosae* focal trees were extremely low (<1.0%, Fig. 3B), but intraspecific takeovers were much higher than anticipated (takeovers by intraspecifics:

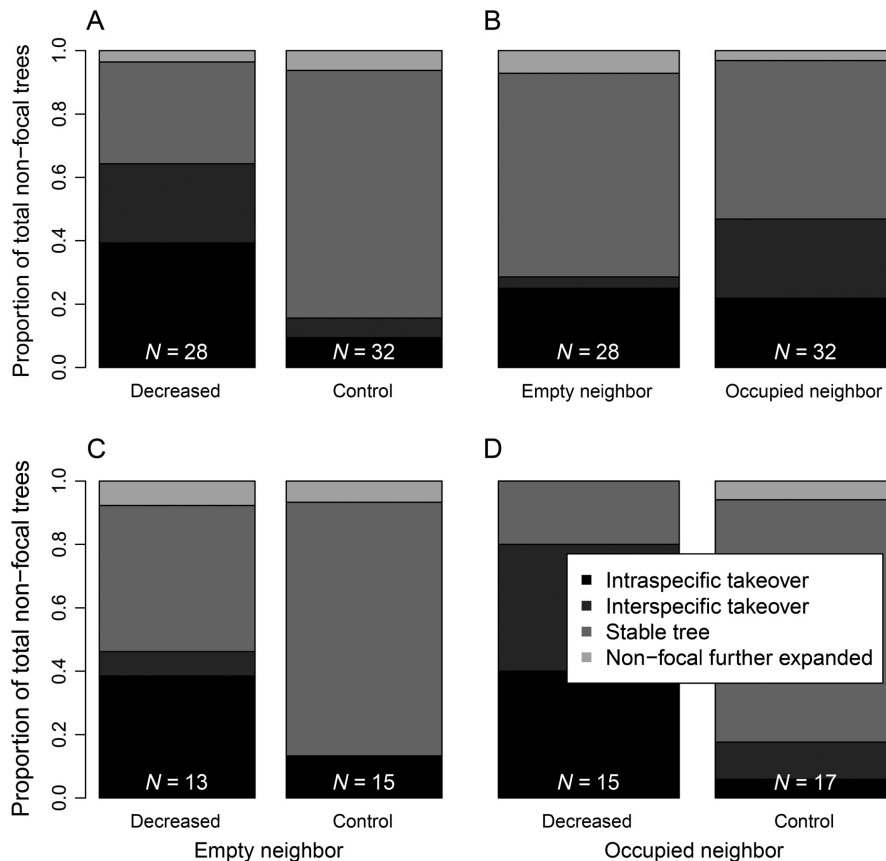


FIG. 4. Proportion of *Crematogaster mimosae* experimental non-focal trees, 12 months after initial expansions, that were stable (inhabited by the original colony determined by genetics), had further expanded (inhabited by original colony, but occupying trees not previously part of an experimental colony), or were taken over by opportunistic intraspecifics or interspecifics. (A) Non-focal tree fate as function of focal density treatment. (B) Non-focal tree fate as function of focal neighbor treatment. (C, D) Non-focal tree fate, split by density treatment, and by whether the focal tree was tied to (C) an experimentally emptied neighbor tree or (D) a heterospecific-occupied neighbor. Since no increased-density treatment was applied to non-focal trees, analyses only compare the decreased-density and control treatments. Sample sizes reflect the total number of non-focal trees, including those from experimental colonies whose focal trees failed to expand, and any recently colonized tree that was not part of an experimental colony at the beginning of the experiment. Intra- and interspecific takeovers were lumped together during logistic regressions to assess non-focal survival success (Table 1C).

emptied-trees 52%, occupied trees 29%; Fig. 3B). In addition, experimentally increasing worker numbers enhanced longer-term expansion of *C. mimosae* colonies beyond the tied-experimental trees. While expansion beyond the focal-tied trees was never recorded among decreased-density colonies, 5% of the control and 20% of the increased-density focal trees did expand beyond the tied trees to occupy one or more trees not originally part of the experimental colony (Fig. 3A–D).

Effects on the fate of non-focal trees

Decreasing worker density on focal trees, and to a lesser degree, manipulating neighbor occupancy, also affected the ability of experimental *C. mimosae* colonies to retain possession of non-focal trees. The original resident *C. mimosae* was significantly more likely to survive in a non-focal tree from a control colony than

if the tree was part of a decreased-density colony (odds ratio = 18.5, $P = 0.001$, Table 1C). The probability of surviving in a non-focal control tree was 0.72 and was 0.35 in a decreased-density colony (Fig. 4A). Overall, expansion success of the focal tree did not predict future vulnerability for the residents of non-focal trees within the same colony (logistic regression, $P = 0.754$, Table 1C). However, 12 months after a focal expansion, experimental colonies appeared to survive better in non-focal trees from colonies that had expanded onto emptied trees 32%, compared to colonies that had defeated an occupied-tree 42% (odds ratio = 4.5, $P = 0.077$, Table 1C, Fig. 4B). In decreased-density colonies in which ants from the focal tree expanded onto an occupied neighbor tree, the experimental colony was more likely to be displaced from non-focal trees (80% of 15 trees were taken over) compared to other treatment combinations, for which takeovers ranged from 13% to 45% (Fig. 4C, D).

DISCUSSION

The behavioral phenotype of a colony emerges from its size, demographics, the individual behaviors of its members, and the impacts of the environment interacting on these attributes (Moore et al. 2002, Fewell 2003, Gordon 2010, Sih et al. 2012). It follows that demographic perturbations are likely to modulate a colony's ability to defend and expand its territory, but experimental studies linking demographic fluctuations to aggression and inter-group competitive success in eusocial species are rare. Filling this gap in our knowledge is important, because social species are foundational elements of terrestrial ecosystems, and interference competition among groups often involves decision-like processes connected to demographic and environmental contexts. For the obligate symbiotic ant *Crematogaster mimosae*, we showed that worker density on host trees is a critical determinant of colony aggression, risk-taking, and competitive dominance over surrounding colonies.

We ascribe differences in aggression and expansion success primarily to changes in worker density because numerous studies support that group size is as a driver of competitive success (e.g., Adams 1990, Wilson et al. 2001, Seddon and Tobias 2003, Tanner 2006). However, it is possible that our manipulations affected other group characteristics that indirectly influenced aggression. For instance, by modifying the number of habitable domatia we could have altered colony perceptions of the relative value of their host trees (see Hepburn and Radloff 1988). This could have increased aggression, but it is unlikely to be the main driver of the differences recorded in our experiment because adding domatia containing workers (increased-density treatment) strongly heightened aggression, but when the colonies were later offered the opportunity to move onto emptied-trees (a proxy for adding empty domatia), aggression levels remained unchanged. Our manipulations could have also altered the ratio of brood to adults, thus promoting higher investment in nest defense (Radford and Blakey 2000, London and Jeanne 2003). This again is unlikely, because our treatments should have had little impact on this ratio given that we either added domatia with all their occupants, or killed both workers and brood.

Short-term effects of density fluctuations

The decisions made by organisms are influenced by the perception of risks and benefits (Maynard-Smith 1982, McGill and Brown 2007, Orrock et al. 2013), and aggression during confrontations often increases with the payoff of winning (Enquist and Leimar 1987, 1990, Green and Field 2011). In ant colonies, worker densities can change dramatically after partial losses of nesting areas or due to mortality during confrontations (Palmer et al. 2000, Trager and Bruna 2006, Rudolph and McEntee 2015). Our manipulations mimicked these naturally occurring abrupt changes in ant density, and

showed that short-term colony competitive success decreases with density and increases with correlates of fighting ability (higher density and aggression). One potential explanation is that our sudden reductions in density negatively impacted encounter rates among workers, thus reducing communication efficiency, and functional cooperation (Pinter-Wollman et al. 2011, Modlmeier et al. 2012). *Crematogaster* workers use odor cues and pheromone trails to recruit nestmates (see Morgan et al. 2004), so decreasing worker densities may have negatively impacted pheromone concentrations or transmission rates, thus reducing cooperation and short-term success. Another possible explanation for our results is that sudden increases in worker density modified colony perceptions of the relative benefits and costs of territorial expansions. In other social species, the perception of resource values, and the aggression towards other groups is linked to relative group sizes (e.g., Anderson and McShea 2001, Harris 2010, Cao and Dornhaus 2013). Larger groups often occupy larger/ richer territories (Tschinkel et al. 1995, Mosser and Packer 2009), so our manipulations could have rapidly changed colony-level perceptions of the benefits and risks associated to expansion opportunities, promoting resource acquisition at higher densities.

Longer-term effects of expansion

Available unoccupied mature trees on this ant-plant system are rare (Young et al. 1997), and our experiment revealed that control and increased-density colonies readily expanded to occupy emptied trees. In contrast, only half of decreased-density colonies expanded despite the lack of imminent mortality risks. These results confirm that trees represent limiting resources for this obligate symbiotic ant, and strongly suggest that territorial expansion is mediated by the combination of short-term, and longer-term perceptions of risks and benefits. Each of the five decreased-density colonies that risked expansion was killed within 12 months by an opportunistic competitor, however, all five colonies that refrained from expansion persisted on focal trees through the year. These starkly contrasting outcomes resemble the fates described for budding or absconding groups in other social insects in which a minimum number of workers is required to ensure successful survival of new groups (see Bouwma et al. 2003, London and Jeanne 2003). It appears that our decreased-density treatment brought colonies of *C. mimosae* near to a critical density threshold of this kind, and that historical fluctuations in worker density might select for periods of conservative, non-expansive behaviors that reduce longer-term colony vulnerability.

Colony vulnerability

All else being equal, decreases in worker density caused by mortality incurred during battles (Palmer et al. 2000,

Palmer 2004, Rudolph and McEntee 2015) should result in greater vulnerability to subsequent takeovers. Our observations did not support this expectation, suggesting the existence of mitigating mechanisms for the loss of workers during conflicts. Some ant species rapidly replenish colony capacity by enslaving heterospecific brood from raided nests (Heinze et al. 1994, Kronauer et al. 2003), but this behavior has not been reported in *Crematogaster*. A more likely explanation is that the eggs and larvae of vanquished colonies constitute high-quality spoils of war that help *C. mimosae* queens replace lost workers quickly. Protein availability is a fundamental determinant of egg production in insects (see Herbers and Banschbach 1998, Aron et al. 2001), and during vulnerable stages a number of species even resort to cannibalism as a strategy to replenish depleted energetic reserves (i.e., Polis 1981, Driessen et al. 1984, Moya-Laraño et al. 2002). Consuming eggs and larvae of defeated enemies can hasten colony recovery, but transforming food into new workers may still take weeks (see Abril et al. 2010), implying some interval of vulnerability after battles.

Assessing the opponent's relative fighting ability prior to a costly confrontation can be critical during vulnerable periods (see Brown et al. 2006), and a variety of insects use visual, chemical, or acoustic displays to measure the likelihood of victory, engaging or avoiding confrontations accordingly (Tibbetts 2008, Tibbetts and Shorter 2009, Innocent et al. 2011). Our results indicate that *C. mimosae* colonies accurately assess relative strengths of surrounding competitors, preferentially attacking colonies whose worker densities are lower relative to their host trees. Compared to unmanipulated colonies in this experiment (23%) and from nearby sites (18–20% turnovers per year), opportunistic takeovers within the decreased-density treatment were extremely high (>90%). Vulnerability assessment among *C. mimosae* colonies might occur through a combination of scout exploratory forays into neighboring territories (encounter frequency), and/or via chemical detection of alarm pheromones (Johnstone 2001, Wood et al. 2002), both of which are likely to be sensitive to changes in worker densities.

Implications for competitive interactions

The competitive coexistence of symbiotic ants in this system is partially explained by priority effects reducing niche overlap among species (see Stanton et al. 1999, Palmer et al. 2002). However, more generally, coexistence is usually promoted by higher levels of intraspecific competition, relative to interspecific competition (Amarasekare 2003, Yang et al. 2010). Prior work in this mutualism has focused primarily on the intensity of interspecific competition (Palmer et al. 2000, 2010, Stanton et al. 2002), but here using genetic markers we reveal that intraspecific competition in *C. mimosae* is pervasive. The much higher rate of intraspecific attacks on experimental colonies relative to aggressions by other species, suggests

that *C. mimosae* is especially good at tracking and exploiting reductions in worker density among conspecifics. Further, Rudolph and McEntee (2015) recently showed that *C. mimosae* can sometimes assimilate brood and workers from defeated conspecific colonies, and in rare occasions temporarily adopt fertile queens. The combination of surveillance capability and capacity for partial assimilation of defeated conspecifics is likely to mitigate the costs of intraspecific competition in *C. mimosae* by allowing it to rapidly recover worker numbers (see Costa and Ross 2003). Over long periods of time, this dynamic could generate negative density-dependence and reduce dominance of *C. mimosae* colonies, thus decreasing the competitive exclusion of subordinate species from this acacia–ant guild.

This study makes several novel contributions to our understanding of ant–plant symbioses and the ecology of social insect communities. First, we demonstrate that colony-level changes in worker density impact group aggression, long-term vulnerability, and colony perceptions of opportunity and risk. At low densities *C. mimosae* colonies are extremely vulnerable to takeovers, and adopt a conservative, non-expansive strategy in order to survive vulnerable periods. Given that host trees are in short supply in this system, our results imply that colony expansion behavior is shaped by the immediate opportunity to secure a limited resource, but also by longer-term risks. Second, by combining experimental manipulations with longitudinal genetic surveys we add a new dimension to previous work emphasizing competition and coexistence among plant–ant species. Specifically, we suggest that the ability of *C. mimosae* colonies to adopt brood, workers, and fertile queens from defeated conspecific colonies (Rudolph and McEntee 2015) may alter the balance between intraspecific and interspecific competition by promoting conflict within this co-dominant species, and reduce the ability of *C. mimosae* to succeed over subordinates. Our ongoing, long-term monitoring of the genetics and demographics of *C. mimosae* colonies, complemented by studying colony-level responses to manipulations of host tree quality, will clarify the factors modulating colony expansion and the balance between intraspecific and interspecific competition in this emerging model system.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1245/full>

DATA AVAILABILITY

Data associated with this paper is available in the Dryad Data Repository: <https://doi.org/10.5061/dryad.b60v7>