

Behavioral Ecology (2013), 00(00), 1–8. doi:10.1093/behco/art069

Original Article

Prey handling performance facilitates competitive dominance of an invasive over native keystone ant

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Received 22 February 2013; revised 20 May 2013; accepted 27 June 2013.

Studies of species coexistence in ant communities often suggest that competitive interactions are mediated by behavioral trade-offs between resource discovery and dominance. However, these studies have always measured foraging at artificial, static baits that omit traits of living prey items and potential coevolutionary predator–prey relationships. In a series of lab experiments, we compare the ability of ants to harvest live termites (*Reticulitermes virginicus*) in nests varying in defensive ability. Moreover, we compare foraging performance of 2 co-occurring ant species—the North American native *Aphaenogaster rudis* and the invasive *Pachycondyla chinensis*—differing in their evolutionary experience hunting *R. virginicus*. Our results show how the invasive *P. chinensis* may displace the native keystone *A. rudis* by directly killing *A. rudis* workers and reducing termite prey available for *A. rudis*. Specifically, *P. chinensis* is more sensitive to novel termite prey than the native *A. rudis* and then destroys termite colonies—even if they are highly defended by soldiers or nest architecture. Our results further show how whole colony behavioral dominance by *P. chinensis* is mediated by behavioral interactions among individual workers. More generally, our experimental approach using live prey to study interspecific competition can integrate evolutionary dynamics into studies of proximate behavioral factors governing species coexistence.

Key words: *Aphaenogaster rudis*, Asian needle ant, discovery–dominance trade-off, invasive species, *Pachycondyla chinensis*, Subterranean termite.

INTRODUCTION

Ecologists studying ant communities have long examined the ways competition for limited resources shapes species coexistence (Brian 1965; Case and Gilpin 1974; Kaspari 1996; Parr et al. 2005; Shik and Kaspari 2010). These studies have often found that species interactions are mediated by trade-offs between the ability to behaviorally dominate resources and other aspects of foraging performance (Davidson 1998; Lebrun and Feener 2007; Lessard et al. 2009). For instance, species in many communities exhibit a negative correlation between exploitative and interference competitive ability (the discovery–dominance trade-off) (Fellers 1987; Davidson 1998; Holway 1999). A more recent goal has been to examine the ways this trade-off is context dependent (Parr and Gibb 2012). For instance, the discovery–dominance trade-off can be maintained when dominant species are constrained by extrinsic factors like temperature (Thomas and Holway 2005), host-specific parasitoids (LeBrun 2005; LeBrun et al. 2007), and habitat complexity (Sarty et al. 2006; Gibb and Parr 2010).

Properties of harvested resources can also govern species interactions. For instance, larger resources can be harder to remove and thus dominate (LeBrun 2005; Lebrun and Feener 2007), while resource quality can mediate discovery rates (Pearce-Duvel and Feener 2010). Here, we examine how prey behavior mediates competitive interactions between ant species. To our knowledge, all previous studies have measured foraging at baits—static resources like honey, tuna, and cat food—and thus omit traits of living prey items that may shape ant discovery and dominance. These experimental resources have also been artificial, and for predatorial ant species thus overlook the role of coevolutionary relationships between predators and prey (e.g., use of specialized chemical cues when hunting; Longhurst and Howes 1978; Schatz et al. 2003). Here, we compare the ability of ants to harvest live termites (*Reticulitermes virginicus*) in nests varying in defensive ability. We further compare foraging performance of 2 co-occurring ant species differing greatly in their evolutionary experience hunting *R. virginicus*, which is native to the forests of the northeastern United States (Banks and Snyder 1920; Austin et al. 2006).

We focus on 2 ant species. *Aphaenogaster rudis* (part of a species complex, hereafter *A. rudis*) is considered a keystone species (Rodriguez-Cabal et al. 2012) native to northeastern United

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States forests, where it harvests and disperses seeds (Beattie and Culver 1981) and insects (Tillberg et al. 2006; Lubertazzi 2012), including termites (Buczowski and Bennett 2007). The Asian needle ant, *Pachycondyla (Brachyponera) chinensis*, is a ponerine with a venomous sting (Nelder et al. 2006) that is native to tropical regions of Australasia (Wheeler 1930) but was introduced into the southeastern United States in the early 19th century (Smith 1934). Since that time, *P. chinensis* has emerged as an important invasive species, with the unusual ability (for invasive ants) to dominate habitats in relatively undisturbed forests (Guenard and Dunn 2010). *Pachycondyla chinensis* is an important predator of termites in the genus *Reticulitermes* in both its native (Matsuura 2002) and invaded (Bednar and Silverman 2011) range. In addition, *A. rudis* populations often decline following *P. chinensis* invasions (Guenard and Dunn 2010), with cascading negative effects on seed dispersal mutualisms (Rodriguez-Cabal et al. 2012).

By using live termite prey native to the same forests as *A. rudis*, we test 2 hypotheses about prey handling performance in these ant species. The first hypothesis holds that *A. rudis* has greater potential to have evolved strategies for detecting co-occurring prey items and then overcoming prey defenses (e.g., soldier castes in termite colonies). An alternative hypothesis proposes that *P. chinensis* displaces *A. rudis* in forested habitats by, at least in part, discovering and dominating resources more effectively than the native species and/or directly killing the native ant, like other successful invasive ants (Holway et al. 2002). Faster discovery by *A. rudis* will support the first hypothesis based on evolutionary experience, given that it has likely foraged for *R. virginicus* termites for many thousands of years longer than *P. chinensis*. In contrast, resource dominance by the newly invasive *P. chinensis* will support the alternative hypothesis based on the traits of other successful invasive species.

To test these hypotheses, we use a series of controlled laboratory experiments that compare the ability of *A. rudis* and *P. chinensis* to 1) discover termite nests and then harvest live termite prey when termite nests vary in amount of 2) behavioral defense by soldier castes, 3) and structural defense through nest architecture. In addition, we examine the behavioral mechanisms by which *P. chinensis* excludes *A. rudis* populations in natural ant communities, using controlled lab experiments to compare behavioral dominance of individual workers, and whole colonies competing for access to termite nests.

METHODS

Foraging natural history

Although both *P. chinensis* and *A. rudis* consume termites (Buczowski and Bennett 2007; Bednar and Silverman 2011; Lubertazzi 2012), it remains difficult to study foraging interactions in the field because these species rarely occur in sympatry following a *P. chinensis* invasion (Guenard and Dunn 2010). However, both species can be among the most locally abundant species in North American hardwood forests. Workers of *A. rudis* are timid and use pheromone laden trails to recruit <10 workers to resources over relatively short distances (ca. 57 cm; Lubertazzi 2012) from small nests that often have <200 workers (Lubertazzi 2012). However, high nest densities can yield >400 *A. rudis* workers per square meter (Talbot 1957). *Pachycondyla chinensis* can also reach high local densities by simultaneously occupying multiple nests hidden within logs, under stones, and in leaf litter (i.e., polydomy). Both species also exhibit specialized foraging behaviors. Workers of *P. chinensis* often use “tandem

carrying” (Guenard and Silverman 2011) to hasten recruitment to resources, whereas workers of *A. rudis* often drop debris on liquid resources, which prevents drowning and can even enhance competitive performance at baits (Fellers and Fellers 1976; Banschbach et al. 2006). It is unknown how these foraging strategies shape competitive interactions between these species.

Collection and maintenance of colonies

We collected colonies of *A. rudis* ($N = 50$ colonies each with a queen and ≥ 75 workers), *P. chinensis* (5 large multiqueen nests), and *R. virginicus* (hereafter “termites”) (5 large nest fragments) from rotting logs in a habitat dominated by 10- to 70-year-old loblolly pine (*Pinus taeda*) in Schenck Memorial Forest (Raleigh, NC; 35°81'N, 78°72'W). Colonies of *P. chinensis* and termites were slowly extracted from wood debris back in the lab. *Pachycondyla chinensis* colonies were housed in large fluon-coated bins where they moved into moist plaster nests in Petri dishes. Termites were housed in bins filled with woody debris and smaller Petri dishes filled with a cellulose matrix. All ant colonies were provided 10 termite workers daily, ad lib artificial diet (Bhatkar and Whitcomb 1970), and water in cotton-plugged tubes and maintained at 26.7 °C and 80% relative humidity, and a 12:12 light:dark cycle.

Resource discovery

We compared the ability of *P. chinensis* and *A. rudis* colonies (100 workers, 1 queen, and 10 brood) to discover termite nests. Each termite colony (198 workers and 2 soldiers) nested in a Petri dish (60 × 15 mm) filled with moist pine wood sawdust placed inside a plastic container that was connected in series to a container with an empty Petri dish (50 × 9 mm) and then one with an ant colony nesting in a moist plaster-filled Petri dish (100 × 15 mm) (Figure 1). Unless otherwise noted, we used these Petri dish sizes for all experiments and connected nest containers with 8 mm lengths of Tygon® tubing (2-mm inner diameter). We also included a control treatment using the same setup, but without termites to examine whether ants entered termite nests to harvest prey or colonize a new nesting area ($n = 5$ per ant species, +/- termite treatment). Termite nest entrances were blocked 24 h before the experiment. During this experiment, ant colonies received ad lib 25% sucrose solution and freshly killed German cockroaches, *Blattella germanica*.

Each hour for 24 h, we recorded 2 foraging variables during 4-min observation periods: 1) number of ants outside the nest (*total foraging*), 2) number of ants in the termite nest (*termite foraging*), and used these to calculate 3) *activity-adjusted termite foraging* (termite foraging/[total foraging + 1]). A mixed-model generalized linear model (GLM) (SAS V.9.2, Cary, NC) was used to analyze the effects of the fixed factors ant species, termite treatment, and time on the 3 foraging variables. This analysis used a split plot design, with ant species and termite treatment as main plot factors and time (a repeated measure) as a subplot factor. We applied the square root transformation prior to analyses of activity-adjusted foraging.

Harvesting defended prey

We examined termite predation by individual ants, placing a single termite worker or soldier in a fluon-coated 50-mL beaker arena and adding a single *P. chinensis* or *A. rudis* worker after 1 min ($n = 30$ per ant species, termite caste pairing). Each trial was ended after termite death or 25 nonfatal ant-termite encounters. In each trial, we recorded 1) encounter number (i.e., events where the ant bit, lunged at, or stung the termite), 2) if the termite died, and 3) the

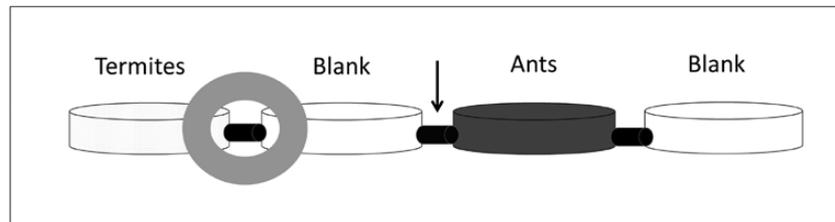


Figure 1

Experimental design for observing ant foraging behavior in the presence and absence of termites. The arrow indicates the blockage point during the 24-h acclimation period. The doughnut indicates the position where observations were recorded.

time from first encounter until termite death. A Cochran–Mantel–Haenszel test was used to examine the effect of ant species on termite survival, controlling for the caste identity. We then used the SAS glimmix procedure, assuming a negative binomial distribution, to examine the effects of ant species and termite caste on encounter number, adjusting for the termite survival outcome. This was done because encounter number was lower when an ant killed a termite ($F_{1,112} = 34.42$; $P = 0.0001$). For trials where termites died, time until death was analyzed using Anova.

We next examined the ability of ant colonies ($n = 14$ *A. rudis* and $n = 17$ *P. chinensis*) to attack termite nests varying in defense by soldier caste. Each nest of 100 worker ants and queen had access to a termite nest containing 200 individuals with either low (1% soldiers), medium (5% soldiers), or high (10% soldiers) defense. Ant colonies were provided ad lib 25% sucrose solution and freshly killed cockroaches during this experiment. Ants in moist plaster Petri dish nests and termites in sawdust-filled Petri dish nests were isolated for 24h, during which time termites constructed carton tunnels. Nests were then connected and termite mortality recorded for more than 7 days.

We used the Henderson–Tilton formula (Henderson and Tilton 1955) to adjust for control termite mortality measured in 13 control nests not exposed to ants. The adjusted proportion of termites killed by ants is calculated as $[1 - (C_1 \times T_F)/(C_F \times T_1)]$, where C_1 and T_1 are numbers of termites in initial control and treated nests, respectively, and C_F and T_F are final termite numbers in these nests. We used 0% mortality in 4 cases where termites paired with ants had less mortality than in control nests. We tested whether ant species differed in termite predation relative to caste defense treatments using a mixed-model GLM on arcsine-transformed termite mortality after 7 days.

Next compared was the ability of *P. chinensis* and *A. rudis* to overcome structural nest defenses when harvesting termites. Adapting the methods of Buczkowski and Bennett (2008), we placed approximately 10 000 *R. virginicus* workers in a large container filled with moist soil and allowed them to colonize pine wood blocks (15 cm \times 4 cm \times 2 cm). After 60 days of gallery construction, termites were extracted by drying the wood blocks under a fluorescent light and then rehydrating blocks by soaking in diH₂O for 24h. We then compared the ability of ant colonies to harvest termites in high defense wooden block nests and low defense termite nests built in Petri dishes (100 \times 15 mm) filled with moist soil and a piece of 78-cm² filter paper.

Two hundred termites (190 workers and 10 soldiers) were allowed to colonize high ($n = 13$) and low ($n = 5$) defense nests and then these were placed in large plastic fluon-coated containers filled with 442 cm² of moist sand. These were then connected to containers that had an ant colony (100 workers, 1 queen, and 50 brood)

housed in a wood block to standardize nest areas. Ant colonies were isolated with ad lib 20% sucrose solution and 10 termite workers for 24h before experiments. After 7 days, we gradually dried termite nests to extract termites and count the survivors. As before, a control treatment ($N = 18$ nests) without ants was included to establish baseline termite mortality and the Henderson–Tilton mortality adjustment applied. In one case where termite mortality with ant predators was less than control, 0% mortality was used. A mixed-model GLM with ant species identity and nest defense level as fixed factors was used to examine the effects on arcsine-transformed termite mortality.

Competitive dominance

We examined the behavioral dominance of individual ants using fluon-coated beaker arenas in which a *P. chinensis* or *A. rudis* worker was placed, letting the “resident ant” acclimate 60 s before adding the “intruder.” *Pachycondyla chinensis* was the resident ant in 12 trials and *A. rudis* in 18 trials ($N = 30$). Each trial lasted until either 25 encounters or an ant death was recorded. We measured 1) the number of encounters, 2) the outcome (death of *A. rudis*, *P. chinensis*, or both alive), and 3) the time from first contact until ant death. As in ant–termite trials, encounter number trended lower if an ant died ($F_{1,25} = 3.64$; $P = 0.07$), so the glimmix procedure in SAS with a negative binomial distribution was used to examine the effects of resident identity on encounter number, adjusting for survival outcome. Time from first encounter to ant death was analyzed using Anova.

We then examined the ability of competing colonies to dominate termite resources by connecting 3 plastic containers (25 \times 15 \times 11 cm) in series, each with a moist wood block with empty termite galleries and 75 mL of moist (1:1; V:V) cellulose. The center container had a termite nest (ca. 1000 termites, 1% soldiers) ($n = 10$) or an empty wooden block ($n = 10$). The +/- termite treatment was used to test whether prey increased ant colony foraging and thus antagonistic interactions between foraging workers. The 2 distal containers contained an *A. rudis* or *P. chinensis* colony matched for size (mean \pm SD: 150 \pm 62.6 workers, 1 queen, and 10 brood) and 1.5-mL artificial diet. Ant nest entrances were blocked for 24h before the start of trials to allow for colony acclimation.

After 80 min, and after 1–3 days, we recorded the number of workers of each species in both the termite and competitor ant nest, as well as the number of dead ants, which were removed. We calculated colony foraging rates by dividing the number of foraging ants by colony size, adjusted for daily mortality, and arcsine transformed this variable prior to analysis. A mixed linear model where termite treatment, foraging location, ant species identity, and time were fixed factors was used to analyze the main and interaction effects. Colony identity was included as a random factor

nested within termite treatment. Time was considered a repeated measure with a compound symmetry defined for its variance–covariance structure. The analysis of colony mortality was similar, but without a location effect because this variable was reported for each ant species for each trial.

RESULTS

Resource discovery

The studies of resource discovery support the hypothesis that *P. chinensis* excludes *A. rudis* in forested habitats by discovering and dominating resources more effectively than the native *A. rudis*. First, *A. rudis* did not have faster initial termite nest discovery than *P. chinensis* ($F_{1,16} = 0.67$; $P = 0.42$), despite having longer coevolutionary experience hunting *R. virginicus*. Furthermore, for more than 24h, *P. chinensis* had higher total foraging ($F_{23,368} = 1.59$; $P = 0.04$), termite nest foraging ($F_{23,368} = 4.22$; $P = 0.0001$), and activity-adjusted termite nest foraging ($F_{23,368} = 4.33$; $P = 0.0001$) (Table 1). In each analysis, significant 3-way interactions occurred between ant species, termite treatment, and time (Table 1), which were driven by higher *P. chinensis* foraging soon after the experiment began in treatments containing termites relative to other treatments without termites (Figure 2).

Harvesting defended prey

Studies of behavioral dominance indicated that 1) *P. chinensis* workers were more effective predators than *A. rudis* against termites of both castes in 1 on 1 trials, killing more termite workers (100%) and soldiers (86%) than *A. rudis*, which killed 7% termite workers and 17% soldiers ($\chi^2 = 77.96$; $P = 0.0001$) and 2) *Pachycondyla chinensis* required fewer encounters to kill termites (1.7 ± 0.2) than *A. rudis* (2.4 ± 0.8), and killed at faster rates (22.0 ± 4.9 s) than *A. rudis* (100.9 ± 15.2 s) ($F_{1,58} = 24.28$; $P = 0.0001$), with no difference between castes in time until death ($F_{1,58} = 0.52$; $P = 0.48$).

This behavioral dominance of workers extended to interactions between whole colonies, with *P. chinensis* killing greater proportions of termites than *A. rudis* ($F_{1,13.8} = 261.55$; $P < 0.0001$) (Figure 3A). Numerous isolated termite head capsules were identified in nests occupied by both ant species indicating that these prey were consumed after being stung and retrieved. Termite mortality was not reduced with higher soldier numbers ($F_{2,13.5} = 2.16$; $P = 0.15$) when preyed on by either ant species ($F_{2,13.5} = 2.84$; $P = 0.09$) (Figure 3A). Although level of structural nest defense did not cause overall differences in termite mortality ($F_{1,32} = 0.27$; $P = 0.60$), there was a significant interaction with ant species identity ($F_{1,32} = 7.79$; $P = 0.009$). This was driven by *P. chinensis* colonies causing greater termite mortality than *A. rudis* ($F_{1,32} = 6.18$; $P = 0.01$), especially in sand nests (Figure 3B).

Competitive dominance

Our results highlight causal links between the suite of *P. chinensis* invasive behaviors and declining *A. rudis* populations in nature. First, *P. chinensis* directly kills individual *A. rudis* workers. Ant death occurred in 43% (13/30) of 1 on 1 trials, with *A. rudis* dying 92% (12/13) of the time. *P. chinensis* workers were equally deadly as the resident and intruder ($\chi^2 = 1.77$; $P = 0.18$), although *P. chinensis* killed faster when it was the resident ($46 \text{ s} \pm 25 \text{ SD}$; $N = 7$ kill events) than when it was the intruder ($75 \text{ s} \pm 38 \text{ SD}$; $N = 5$ kill events) (residentID \times deathID [alive]: $F_{3,25} = 7.98$; $P = 0.0007$).

Second, *P. chinensis* had higher foraging rates than *A. rudis* when both simultaneously competed for termites ($F_{1,120} = 31.19$; $P = 0.0001$; Table 2), with this effect being driven by large numbers of *P. chinensis* entering termite nests ($F_{1,120} = 5.97$; $P = 0.02$; Table 2) (Figure 4). In addition, approximately 5% of each *P. chinensis* colony consistently foraged in the competing *A. rudis* nest (Figure 4), and *P. chinensis* workers could be seen transferring dead *A. rudis* workers to their nests. This harvest of *A. rudis* workers occurred even without termites ($F_{1,8} = 0.31$; $P = 0.59$; Table 2). As a result, *A. rudis* colonies rapidly declined in size ($F_{1,8} = 14.86$; $P = 0.005$; Table 2) even in the absence

Table 1
Resource discovery experiment

Effect	Treatment	Num. df	Error df	F	P
Total foraging	Ant species	1	16	0.00	0.97
	Termite treatment	1	16	2.17	0.16
	Ant \times termite	1	16	0.60	0.45
	Time	23	368	3.59	0.0001
	Ant species \times time	23	368	1.59	0.04
	Termite \times time	23	368	1.13	0.31
	Ant \times termite \times time	23	368	2.17	0.002
Termite nest foraging	Ant species	1	16	8.31	0.01
	Termite treatment	1	16	0.80	0.38
	Ant \times termite	1	16	0.41	0.53
	Time	23	368	2.21	0.001
	Ant species \times time	23	368	4.22	0.0001
	Termite \times time	23	368	1.77	0.02
	Ant \times termite \times time	23	368	1.93	0.007
Activity-adjusted termite foraging	Ant species	1	16	42.72	0.0001
	Termite treatment	1	16	0.00	0.96
	Ant \times termite	1	16	0.23	0.64
	Time	23	368	1.82	0.01
	Ant species \times time	23	368	4.33	0.0001
	Termite \times time	23	368	0.95	0.53
	Ant \times termite \times time	23	368	1.79	0.01

df, degrees of freedom. Results of mixed-model GLM analyzing how ant species identity (*Aphaenogaster rudis* or *Pachycondyla chinensis*), termite treatment (+ or –), and time (hourly observations for more than 24h) shape ant foraging. See Methods for details.

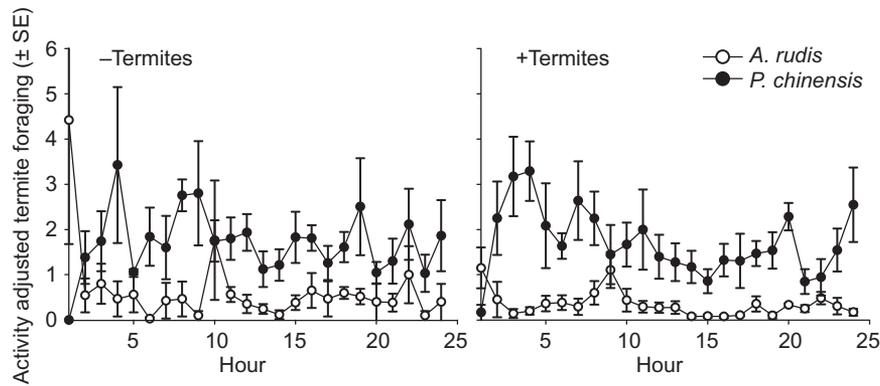


Figure 2

Foraging for more than 24 h of *Aphaenogaster rudis* and *Pachycondyla chinensis* colonies with and without termites in the nest. Activity-adjusted termite foraging is the termite foraging divided by the number of ants outside the colony at each time interval.

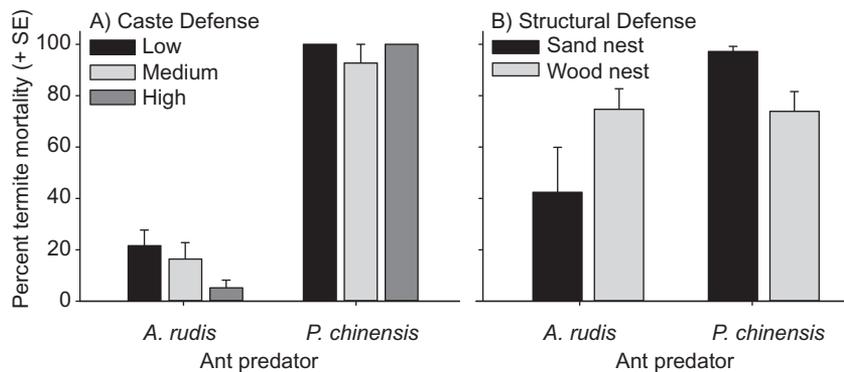


Figure 3

Termite mortality after 3 days when exposed to predatory ant colonies under different levels of (A) behavioral defense by termite soldiers and (B) structural defense.

of termites ($F_{1,8} = 0.01$; $P = 0.92$; Table 2) (Figure 5). Thus, *P. chinensis* excluded *A. rudis* colonies through exploitative competition by harvesting termites at greater rates and interference competition by directly killing and harvesting *A. rudis* workers.

DISCUSSION

Our results support a hypothesis that the behavioral traits making *P. chinensis* a successful invasive termite predator trump the evolutionary experience of *A. rudis*. *Pachycondyla chinensis* colonies foraged for termites at higher rates and caused higher termite mortality, even if nests were highly defended by soldiers or architecture. This whole colony dominance was mediated by the aggression of individual *P. chinensis* workers that killed more termite workers and soldiers than *A. rudis*, and in less time. Moreover, our results provide insights into the behavioral dynamics by which *P. chinensis* is thought to exclude *A. rudis* colonies in nature, by both reducing termite prey available for *A. rudis* and directly killing *A. rudis* workers. By using live prey to study ant foraging performance, we examine whether ants overcome not only the behavioral defenses of competitors but also prey items (soldier castes and nest architecture) and thus place dominance–discovery trade-offs in the context of coevolutionary dynamics between predator and prey.

This controlled laboratory study provides a unique window into the mechanisms by which *P. chinensis* displaces *A. rudis*, a keystone

species, in mature undisturbed forests (Guenard and Dunn 2010; Rodriguez-Cabal et al. 2012). A series of focused experiments uses live termite prey items to isolate key behavioral interactions among workers that can be difficult to observe in the field and then scales these up to understand mechanisms governing whole colony behavioral dominance. However, we also acknowledge the limits on extrapolation that accompany any lab experiment. For instance, ant interactions were constrained by the space in experimental arenas and we may thus have overestimated the impacts of *P. chinensis* aggression (i.e., *A. rudis* may avoid conflict in the field by running away). In addition, although *A. rudis* colonies were collected in their entirety, *P. chinensis* worker numbers were more difficult to estimate because *P. chinensis* colonies are polydomous. Moreover, we may have overestimated the strength of interference competition, given that *A. rudis* colonies may persist by exploiting alternative foods not harvested by *P. chinensis* (e.g., seeds; Lubertazzi 2012). And yet, given that *A. rudis* is absent from forests invaded by *P. chinensis*, it is not a stretch to predict that the domination of food and direct aggression displayed by *P. chinensis* in the lab explain dynamics observed in the field.

Although *P. chinensis* shares traits with other invasive ant species, we caution that the conclusions drawn from our experiments may not necessarily extend to other native/invasive species dynamics. The assumption that competition mediates species coexistence has long served as a starting point in ecological studies of ant

Table 2
Colony dominance experiment

Effect	Treatment	Num. df	Error df	F	P
Ant foraging	Termite treatment	1	8	0.31	0.59
	Location	1	120	7.87	0.006
	Termite × location	1	120	0.05	0.83
	Ant species	1	120	31.19	0.0001
	Termite × ant sp.	1	120	0.89	0.35
	Location × ant sp.	1	120	5.97	0.02
	Termite × location × ant sp.	1	120	0.34	0.56
	Time	3	120	0.81	0.49
	Termite × time	3	120	1.11	0.35
	Location × time	3	120	3.94	0.01
	Termite × location × time	3	120	0.24	0.87
	Ant species × time	3	120	0.82	0.49
	Termite × ant sp. × time	3	120	1.05	0.37
	Location × ant sp. × time	3	120	3.33	0.02
	Termite × location × ant × time	3	8	0.12	0.95
Worker mortality	Termite treatment	1	8	0.01	0.92
	Ant species	1	8	14.86	0.005
	Termite × ant sp.	1	32	0.06	0.82
	Time	2	32	32.72	0.0001
	Termite × time	2	32	0.19	0.83
	Ant sp. × time	2	32	13.42	0.0001
	Termite × ant sp. × time	2	32	0.32	0.73

df, degrees of freedom. Results of mixed-model GLM analyzing the effects of termite treatment (+ or -), location (termite nest or competitor ant nest), ant species identity (*Aphaenogaster rudis* or *Pachycondyla chinensis*), and time (observations after 1–3 days) on ant foraging. See Methods for details.

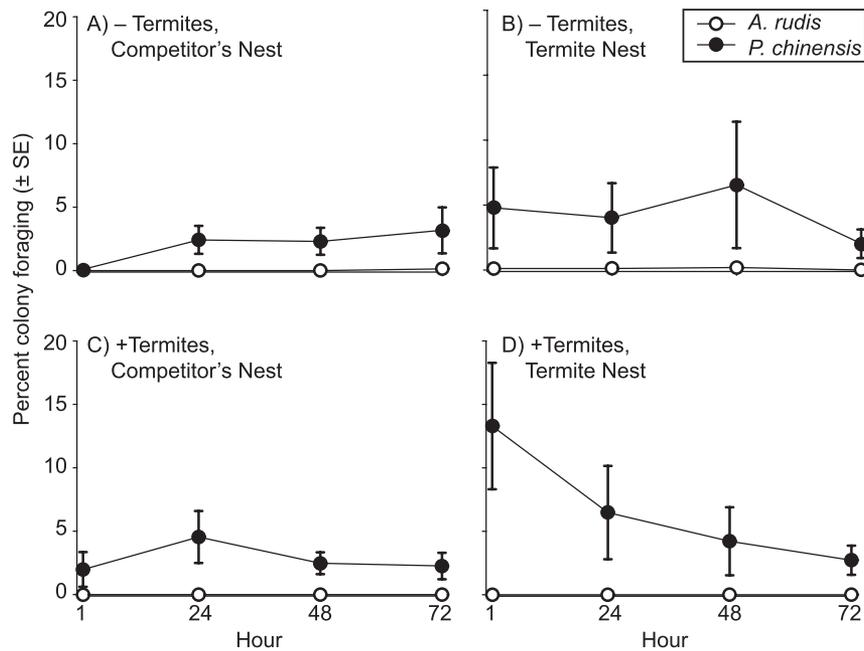


Figure 4

Activity levels of *Aphaenogaster rudis* and *Pachycondyla chinensis* when simultaneously foraging in competition experiments. We measured foraging (A) without termites at the competitor's nest, (B) without termites at the termite nest, (C) with termites at the competitor's nest, and (D) with termites at the termite nest.

communities (e.g., Hölldobler and Wilson 1990; Sanders and Gordon 2003; Parr et al. 2005), and invasive ants have provided model systems to study the underlying mechanisms (reviewed by Holway et al. 2002). However, other studies have found evidence that anthropogenic disturbance (e.g., mowing and plowing; King and Tschinkel 2008) or abiotic factors (e.g., moisture and vegetation cover; Menke and Holway 2006) govern the ecological impacts

of invasive ants. It will thus be important to conduct further experiments manipulating ant colony abundance in the field (as per Gibb and Hochuli 2004; King and Tschinkel 2008) to verify that behavioral dominance observed in the lab translates into community level effects. However, we also note that the *P. chinensis* populations studied here have displaced those of *A. rudis* in mature hardwood forests without any human disturbance for more than

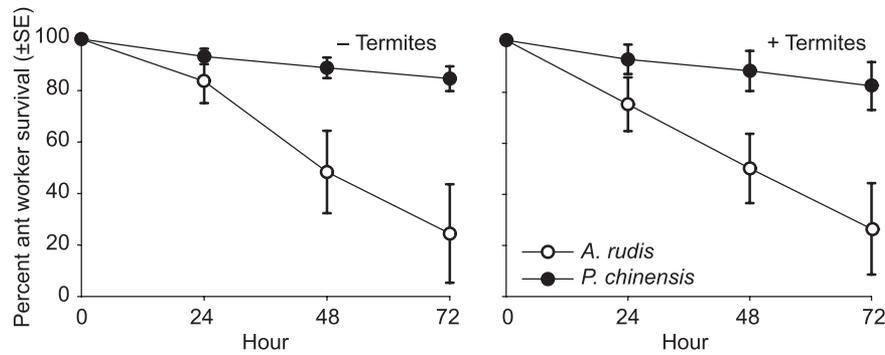


Figure 5

Aphaenogaster rudis and *Pachycondyla chinensis* worker mortality in competition experiments with and without termite prey items.

100 years. This extirpation has also occurred rapidly, within 10 years following *P. chinensis* introduction (Guenard and Dunn 2010). It thus appears likely biotic interactions linked to expanding *P. chinensis* populations, rather than human-mediated disturbance or abiotic constraints caused the *A. rudis* population decline.

Pachycondyla chinensis completely destroyed termite nests in this study—even when termite colonies were highly defended. Behavioral observations further showed *P. chinensis* workers excitedly circled termite nest entrances, stinging emerging termites, and quickly returning them to the nest where they were dismembered. This sensitivity to a novel termite prey suggests that *P. chinensis* relies on strategies used to hunt termites in its native range (Matsuura 2002; Yashiro et al. 2010). Alternatively, the hunting performance of *P. chinensis* may be enhanced because *R. virginicus* lacks evolutionary experience defending against ants from the genus *Pachycondyla*, which contains many termite specialists (Andersen 2000). For instance, *Reticulitermes speratus* termite soldiers from the native range of *P. chinensis* have specialized plug-shaped heads that prevent *P. chinensis* workers from entering their nests (Matsuura 2002). *Pachycondyla chinensis* is an unusual invasive ant in part because it successfully invades relatively undisturbed forested habitats (Guenard and Dunn 2010; Yashiro et al. 2010), and because it is fuelled by hunting live insects (Bednar and Silverman 2011) rather than scavenging for carbohydrate-based resources (Davidson 1998; Rowles and Silverman 2009). It will thus be interesting to examine whether *P. chinensis* invasive success is higher in forests from regions where termite populations lack previous evolutionary experience with *Pachycondyla*.

The fast discovery rates of *P. chinensis* are especially impressive given that *Aphaenogaster* species are often among the first to baits (Fellers 1987) and are known to prey on termites (Buczowski and Bennett 2007, 2008). Evidence suggests that *P. chinensis* detects volatile compounds secreted by *R. virginicus* (Bednar and Silverman 2011), using chemical cues to locate termites like other *Pachycondyla* species (Hölldobler et al. 1996; Garcia Perez et al. 1997). It is possible that *R. virginicus* allelochemicals are similar to those of termites hunted by *P. chinensis* in its native range or that the chemosensory system of *P. chinensis* is highly flexible. Regardless, the result is that *A. rudis* is being replaced by an ant species that responds strongly to termite prey, but not to seeds, with impacts that ramify across forest ecosystems (Bayliss and Fielding 2002; Rodriguez-Cabal et al. 2012).

It will be important to examine how *P. chinensis* termite hunting ability interacts with other traits conferring invasive success, such as its dispersed polydomous nest structure and colonies with many egg-laying queens (Gotoh and Ito 2008). These additional traits can be easily integrated into the experimental approach

developed here, which presents live prey to resident ants. In the case of *P. chinensis* and *A. rudis*, such studies can be extended to compare foraging on termite species native with the range of both ant species (e.g., *R. flavipes*; Beard 1973) or only *P. chinensis* (e.g., *R. speratus*; Matsuura 2002). Moreover, the methods developed here can then be used to test basic assumptions about resource discovery and dominance in the field, and ultimately the extent to which these biotic interactions scale up to shape community structure. The results will help integrate evolutionary dynamics into the study of how proximate behavioral factors shape species coexistence.

FUNDING

Support for this research came from the Blanton J. Whitmire Endowment at North Carolina State University.

We thank R. Dunn and E. Vargo for providing improvements to the manuscript and Consuelo Aurellano for statistical advice.

Handling editor: Anna Dornhaus

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