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Territorial status-quo between the big-headed ant (Hymenoptera: Formicidae) and the Formosan subterranean termite (Isoptera: Rhinotermitidae)

Thomas Chouvenc, Aaron J. Mullins and Nan-Yao Su*

Abstract

The big-headed ant, *Pheidole megacephala* (Fabr.) (Hymenoptera: Formicidae) and the Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae) are 2 invasive species in south Florida, and both have a major economic and ecological impact. Because both species are often associated with man-made structures, we investigated how the 2 species interacted when their tunneling system connected, to determine if the big-headed ant had the ability to predate or displace subterranean termite colonies. It was previously suggested that the 2 species had a predator-prey interaction. However in this study we showed that *C. formosanus* can defend its territory against *P. megacephala* with minimal loss, and we therefore re-described their interaction as a status quo for habitat competition. It is unlikely that a competitive displacement would take place between *C. formosanus* and *P. megacephala* because of their ability to successfully defend their respective nests.

Key Words: *Pheidole megacephala*; *Coptotermes formosanus*; competition; planar arena; displacement

Resumen

La hormiga cabezona, *Pheidole megacephala* (Fabr.) (Hymenoptera: Formicidae) y la termita subterránea de Formosa, *Coptotermes formosanus* Shiraki (Blattodea: Rhinotermitidae) son dos especies invasoras en el sur de la Florida y ambas tienen un importante impacto económico y ecológico. Debido a que ambas especies se asocian a menudo con las estructuras hechas por el hombre, se investigó cómo las dos especies interactuaban cuando su sistema de túneles estan conectados, para determinar si la hormiga cabezona tenía la habilidad de atacar antes o desplazar a las colonias de termitas subterráneas. Fue sugerido anteriormente que las dos especies tuvieron una interacción depredador-presa; sin embargo, en este estudio se demostró que *C. formosanus* pueden defender su territorio frente a *P. megacephala* con una pérdida mínima, y por lo tanto re-describe su interacción como una competencia equilibrada. Debido al éxito ecológico de *P. megacephala*, su presencia en el sur de Florida podría ser interpretado como un factor para disminuir la propagación de las termitas subterráneas invasoras directamente competitivos por el hábitat, pero es poco probable que un desplazamiento competitivo tendría lugar entre *C. formosanus* y *P. megacephala* debido a su capacidad para defender con éxito sus respectivos nidos.

Palabras Clave: *Pheidole megacephala*; *Coptotermes formosanus*; competencia; arena plana; *status quo*

The urban south Florida area hosts a diverse community of social insects with many invasive ants and termites from tropical or subtropical areas (Deyrup 2003; Scheffrahn 2013). The urban landscape is primarily dominated by a several exotic ant species such as the big-headed ant *Pheidole megacephala* (Fabr.) (Hymenoptera: Formicidae) among several hundred ant species, both native and non-native (Deyrup 2003). Invasive subterranean termites also represent a major problem in south Florida with primarily the Formosan subterranean termite *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae) and the Asian subterranean termite *C. gestroi* (Wasmann) (Scheffrahn 2013), owing to the damage they do to man-made structures (Rust & Su 2012). The interaction of invasive species in non-native areas recently received particular interest as the social insect community can be dynamic with one species displacing others (Wells & Henderson 1993; Lebrun et al. 2014).

Pheidole megacephala is one of the most invasive ant species in the tropics, (Wetterer 2012) and was described as a top predator and competitor of other insects (Hoffmann et al. 1999; Dejean et al. 2007), making this species a principal actor in the process of competitive displacement (Debach 1966; Holway & Suarez 1999). In Broward County (Florida), *P. megacephala* has displaced many other ant species and can be locally dominant (Warner & Scheffrahn 2013). As we were investigating the foraging territory of some *C. formosanus* and *C. gestroi* colonies in this area, we noticed that in locations with relatively high densities of *P. megacephala*, subterranean termite colonies would be restricted to structures or trees and could not be sampled from the surrounding soil using regular ground trap techniques (AM; TC, personal observation). Similar observations between *C. formosanus* and *P. megacephala* were made in Hawaii by Cornelius & Grace (1995), as the ants were commonly found in termite collection traps in the field. Nest invasion

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assays in the laboratory previously showed that *P. megacephala* was able to predate and take over *C. formosanus* groups (Cornelius & Grace 1996), but that *C. formosanus* soldiers could temporarily defend access points while workers would establish a wall to block the access to ants (Cornelius & Grace 1997). However, in their experiments, Cornelius & Grace observed relatively high termite mortality as the protocol they used offered little chance for the termite groups to retreat and establish a proper defense in a realistic tunnel system. Recently, one of us observed in the field that both species could coexist within centimeters (Fig. 1) for a period over a year (TC, pers. obs.) which raised questions on the ability of *P. megacephala* to displace *C. formosanus*. We here endeavoured to reassess the ability of *C. formosanus* to defend their territory against *P. megacephala* using planar arenas, which allowed both species to establish their own tunnel system before interaction, to determine if *P. megacephala* has the potential ability to displace *C. formosanus* populations.

Materials and Methods

COLLECTION OF INSECTS

Termites were collected from 3 field colonies of *C. formosanus* in Fort Lauderdale, Florida, using the method described by Su & Scheffrahn (1986), then processed according to Tamashiro et al. (1973), and kept in groups of at least 1,000 for 10 to 15 d in containers stored at 28 °C with blocks of spruce (*Picea sp.).* Ants were collected from field colonies of *P. megacephala* in Fort Lauderdale, by lifting stone plates on the ground showing signs of sand excavation. Sub-colonies were collected by gently brushing the brood, reproductives and worker ants off the stone into individual containers. All ant groups were then transferred to experimental arenas with access to sugar water (25%) and supplied daily with 5-10 termite workers as prey.

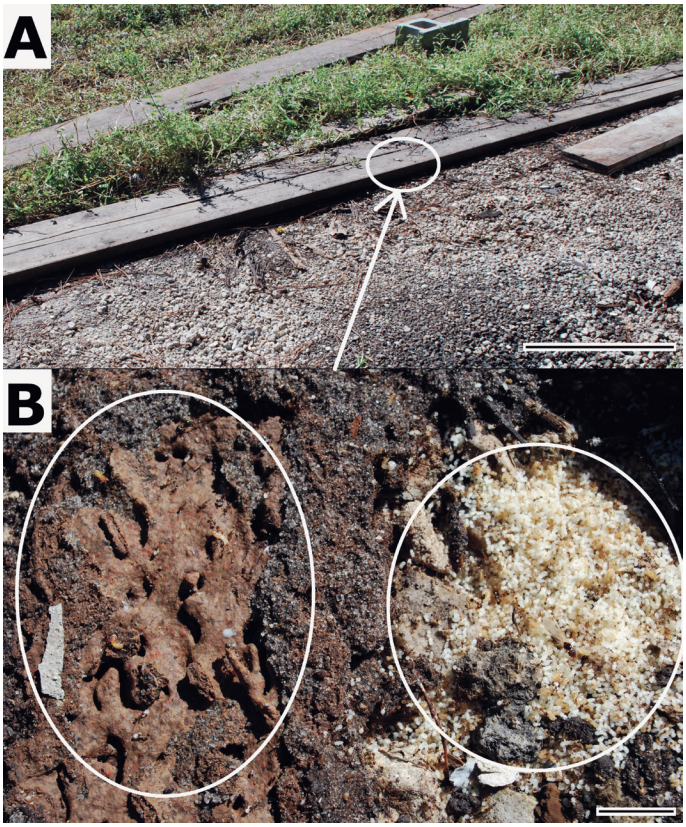


Fig. 1. A) Abandoned lot in a residential area in Ft Lauderdale, Florida. Scale bar = 1 m. **B)** Under the woodblock on the ground, *P. megacephala* had a nest structure with a large brood (circled on the right), while within 5 cm, separated by an insect-made soil barrier, *C. formosanus* had a tunneling structure (circled on the left), here a fecal deposit, at the interface between the soil and the woodblock. The observed agonism between the 2 species was the result of the disturbance when the woodblock was lifted, however, both species were previously observed one year before at this exact location, showing that the proximity between the 2 species can be stable over time. Scale bar = 2cm.

PLANAR ARENAS

The use of planar arenas filled with soil has been described as a functional device that allows subterranean insects to forage and establish their own tunnel system, while allowing for full observation (Chouvenc et al. 2011). In this study, the arenas used were similar to those used by Su (2005). Each arena was composed of 2 transparent acrylic sheets (24 × 24 × 0.6 cm in thickness) separated from each other by plastic laminates (0.2 cm in thickness), creating a 15 × 20 × 0.2 cm internal space. Two pieces of 0.2-cm-thick transparent acrylic strips (7 × 1.5 cm) were bolted between the 0.6-cm-thick acrylic sheets at 3.5 cm from each other near the arena center to maintain the 0.2-cm gap of the arena. A cellulose pad (45 mm diam, 0.2 cm in thickness, Millipore Corp. Billerica, Massachusetts) was placed in the center of the arena as food source and buffer for moisture. Approximately 60 g of sifted sand (150–500-µm sieves) was poured in the 0.2-cm gap and moistened with ≈15 mL of deionized water. The upper acrylic sheet had an access hole (0.5 cm in diam) near one corner, onto which an acrylic cup (4.5 cm in diam and 3 cm in height) with lid was fitted to form an insect release chamber. On both sides of the arena, 2 access holes were provided to connect the arena to foraging sites or to connect 2 arenas together using 30 cm of Tygon® tubing (0.6 cm internal diam) for the experiment (Fig. 2).

ANT-TERMITE COMPETITION EXPERIMENT

Eighteen arenas were prepared, with 9 arenas containing ants, and 9 arenas containing termites (3 each of 3 colonies). In each ant arena ≈330 *P. megacephala* were introduced, including 30 major, 200 minor, 100 brood and 1-2 Queen(s). In each termite arena, 250 *C. formosanus* were introduced, including 225 workers and 25 soldiers. For both species, caste proportions reflected the average proportions collected from the field. Groups of insects were able to establish in individual arenas for 3 d, building a tunnel structure connecting the arena space to foraging sites (wood for termites, sugar water for ants). After 3 d, each termite arena was connected to an ant arena with 30 cm Tygon® tubing filled with moist sand. The interaction between the 2 species

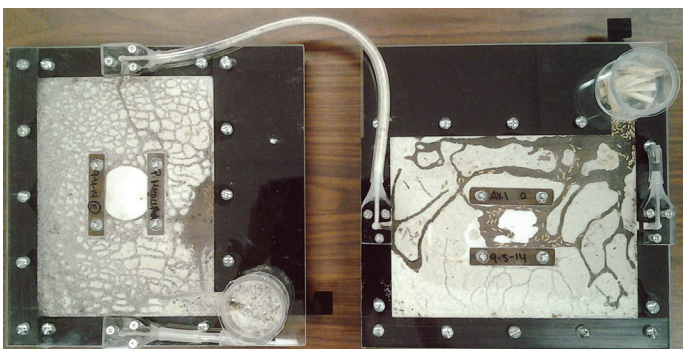


Fig. 2. Arena setup for the competition experiment. On the left, the arena contains the group of *P. megacephala*, while on the right, the arena contains the group of *C. formosanus*. Both arenas are connected by a tube (30 cm).

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Table 1. Results of agonism assay in planar arenas between *P. megacephala* and *C. formosanus.*

	Ants (*P. megacephala*)	Termites (*C. formosanus*)	Statistics
Total number of sealing/opening in all replicates (initiated by)	19	16	$p = 0.5$ (binomial test)
Mortality in 'single access point' replicates ($n = 5$) (number of dead individuals)	22.8 ± 4.8	18.8 ± 5.5	$p = 0.82$ (paired *t*-test)
Mortality in 'invasion' replicates ($n = 4$) (number of dead individuals)	39.7 ±7.6	41.2 ± 9.0	$p = 0.67$ (paired *t*-test)

was recorded for 7 d. Mortality was monitored and sites of agonism were also recorded. In the results, the statistical analysis for the mortality in arenas was split in 2 parts; first, the arenas with no invasions (relatively low causalities), and second the arenas with one species partially invading the arena of the other (relatively high casualties) as the mortality data had a bi-modal distribution for both species. In both cases, mortality between ants and termites was compared using a paired t-test. The number of cases where one given species opened access to the tunnel of the other species was compared with a binomial test.

Results

Within 1h after connecting the arenas, we observed in all replicates that ants and termites were both present in the tubing connecting the pair of arenas. Agonism was observed at the point of contact, usually resulting in a few dead ants and dead termites, and both species initiated the sealing of the tube with sand particles (Fig. 3A). Within a week after the initiation of the species interaction, a series of skirmishes was observed between ants and termites, as the sand seal was periodically reopened by one of the species. A total 37 sealing/opening cycles were directly monitored and the number of re-opening of seals by ants and by termites were not significantly different (19 by ants, 16 by termites, binomial test, $p = 0.5$). In all observations, the fight only lasted a few minutes with only a handful of dead termites and ants, before the opening was sealed again.

The progression of a species toward the arena of the other species was usually negligible, with little territorial invasion by either species, as the irregularity of the tunnels was used as a choke point that could be closed rapidly, as a "safety valve" to prevent invasion. Therefore, within a week, for 5 out of 9 replicates, the confrontation between *P. megacephala* and *C. formosanus* was limited to a single access point in the tubing, or in the arenas within 3 cm of the entrance point of the arena (Fig. 3B). In these 5 cases, an average of 22.8 ± 4.8 ants (mostly minor workers) were killed by the termites and 18.8 ± 5.5 termites (mostly soldiers) were killed by the ants (no significant mortality between the 2 species, paired *t*-test $p = 0.82$) within 7 d. In 2 arenas, termites were able to infiltrate the ant arena (Fig. 4), and in 2 other replicates some ants accessed the termite arena. However, in both events, scouts were rapidly pushed back or killed, and despite a small gain of territory by the invading species, the interaction ceased as the tunnels were sealed again (Fig. 5) and the dynamic *status quo* was re-established as previously observed in the 5 other replicates. Because of the larger number of individuals involved in the agonistic events of the 4 replicates with invasion, casualties were substantially higher, with an average of 39.7 ± 7.6 ants killed (mostly minor workers) and 41.2 ± 9 termites killed (both soldiers and workers) per replicate (no significant mortality between the 2 species, paired *t*-test $p = 0.67$) . We note here that in both cases, the temporary invasion was possible only because of the timing of the opening of the seal by one of the species, where no sentinel was present on the other side at the moment of the breach, allowing for the sudden infiltration (See Fig. 3 for an example of "sentinel" individuals).

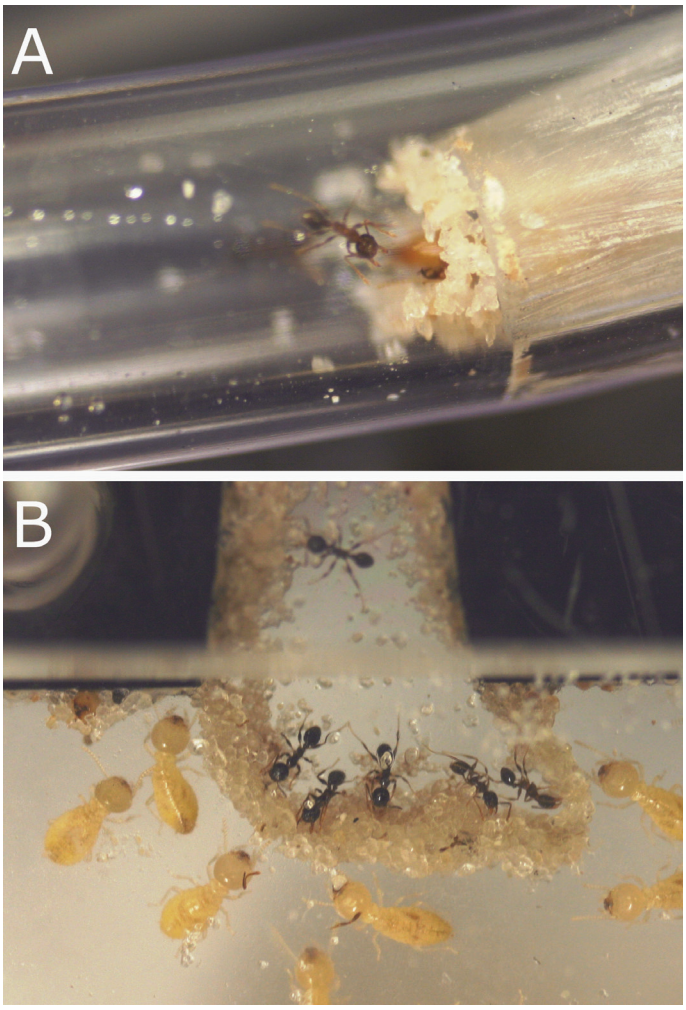


Fig. 3. Sealing and walling off the access point between the 2 species where both termites and ants are depositing sand particles to create a physical separation with little to no casualties. **A)** in the tube between the arenas, **B)** at the entrance of the arena.

Discussion

Our results support the findings of Cornelius & Grace (1996, 1997) that groups of *C. formosanus* can establish a defense against the attack of predators such as *P. megacephala*. However, using planar arenas, we demonstrated that termites have the ability to protect their territory and prevent the ant invasion by losing a minimal number of individuals during the brief interaction and seal off any access. When a seal was broken, a handful of ants and termites fought at the point of contact, while both ants and termites initiated the re-sealing of the tunnel, preventing major battles, and limiting the loss of individuals to a few at the frontline. This observation is similar to the one made by Li et al. (2010) about the interaction between *C. formosanus* and *C. gestroi* in arenas,

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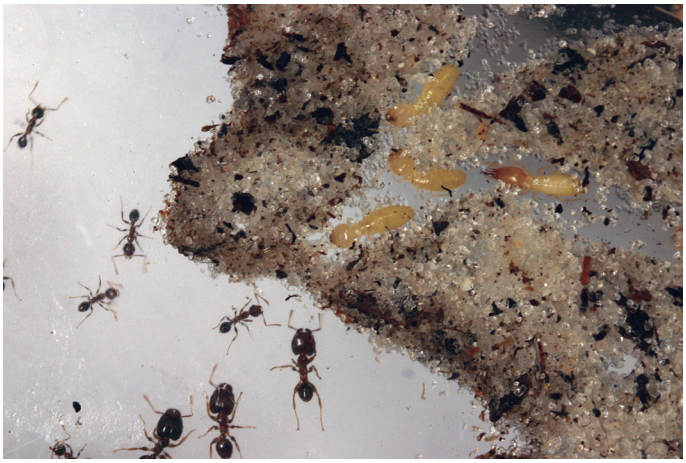


Fig. 4. Termites inside the ant arena. After the termite group accessed parts of the ant tunnel system, ants rapidly sealed all connections to prevent direct interaction.

as the 2 termite species would initiate brief battles at the point of contact of 2 tunnels and seal the access immediately after.

While *P. megacephala* is considered a top predator(Dejean et al. 2007), we here emphasize that *C. formosanus* was able to maintain the status quo, rather than a competitive displacement with the ants, and displayed a level of aggressiveness equal to the ant, by opening the seal and attempting invasion as much as *P. megacephala* did. In fact, our results suggest that *C. formosanus* and *P. megacephala* are true competitors for nesting territory in a soil environment, and their interaction should not be interpreted as a prey-predator system. The ants were not able to take over the termite nest and vice versa, and casualties resulting from the interaction were similar for both species. Because of such results, we here suggest that as long as both colonies are healthy and have a critical mass, they could maintain their existing territory with minimal loss of individuals over time, which supports the observation made in the field (Fig. 1).

As it was suggested that *P. megacephala* colonies could be used as natural enemies against the subterranean termites to help protect structures (Culliney & Grace 2000), our study implies that it is unlikely for *P. megacephala* to fully prevent subterranean termites from infesting a structure. However, *P. megacephala* can form a conglomerate of interconnected colonies (supercoloniality; Tsutsui et al. 2003), and if present around a structure, it may 1) reduce the access to this structure to a mature subterranean termite colony by simple territorial competition, and 2) prevent an existing subterranean termite colony from a structure to expand outward. In such a case, the detection of subterranean termites using ground monitors may be limited in the presence of large populations of *P. megacephala*, as the termite colony may be restricted to a tree or a man-made structure, and this would explain why we often failed to detect *C. formosanus* in ground monitors around a known infested structure when *P. megacephala* was present at relatively high density in the area (TC; AM, pers. obs.).

In addition to our results, we also observed a different type of interaction between the 2 species in the field during termite swarming events. In spring, mature termite colonies release thousands of alates during dispersal flights (Scheffrahn 2013). During these events, we often observed alates of *C. formosanus* and *C. gestroi* land on the ground and be immediately predated, primarily by *P. megacephala* (Fig. 6). We can assume that the survival rate of termite alates and colony foundation are both reduced owing to predation by ants. In this case, *P. megacephala* can negatively impact the ability of termites to disperse by limiting their opportunity to reach a favorable nesting site, and the predator-prey interaction would therefore still be valid at this particular phase of the termite's life cycle.

To conclude, both *C. formosanus* and *P. megacephala* are invasive social insects in south Florida with important economic and ecological impacts. Our results suggest that both species are mutual competitors for nesting habitats and territory, and both have the ability to compete for the same niche (Fig. 1). While *P. megacephala* has been demonstrated to displace many native and non-native social insect communities (Hoffman et al. 1999), we here advocate that *C. formosanus* will "stand its ground", and will remain a major structural pest in this area regardless of the presence of the big-headed ant.

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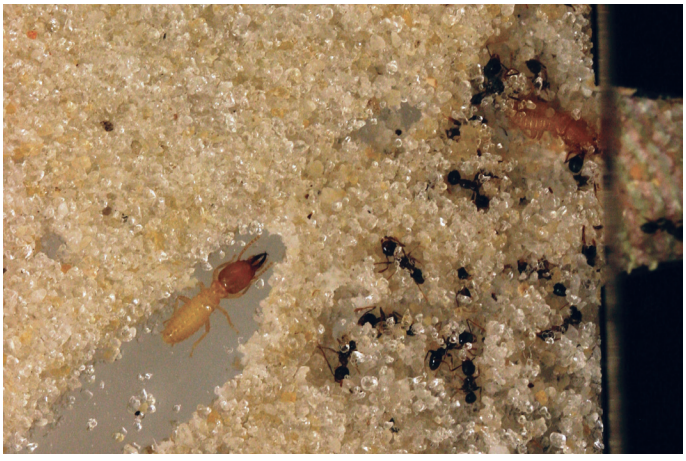


Fig. 5. Accumulation of cadavers in the area with agonistic interaction between ants and termites. At the end of the fight, ants and termites sealed the area to prevent further contact.



Fig. 6. Predation of *P. megacephala* on alates of *C. formosanus* after a swarming event.

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