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# *Pheidole megacephala*: An invasive ant that raids colonies of the red imported fire ant, *Solenopsis invicta*

**Airlan San Juan**[1] | **Frédéric Azémar**[2] | **Alain Dejean**[2,3]

[1]Independent Researcher, keyapa.com, New Brunswick, New Jersey, USA

[2]Université de Toulouse, Toulouse INP, CNRS, IRD, CRBE, Toulouse, France

[3]UMR EcoFoG, AgroParisTech, Cirad, CNRS, INRA, Université des Antilles, Université de Guyane, Kourou, France

**Correspondence**
Alain Dejean
Email: alain.dejean@wanadoo.fr

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The establishment and spread of many imported ant species are facilitated by a high level of reproduction, the future queens mating without nuptial flight so that the colonies reproduce through budding. The colonies are polygynous (i.e., multiple queens) and form unicolonial societies that spread over large areas and reach high densities, often outcompeting native ants through ecological dominance (Suarez et al., 2010; Wong et al., 2023).

These characteristics are present in the well-known invasive species *Pheidole megacephala*, or the big-headed ant, native to tropical Africa. Like most *Pheidole* species, its worker caste is dimorphic with small minors and big-headed majors or "soldiers," both having small stingers that serve only to lay odor trails (Wilson, 2003). In its introduced range, this species forms large, unicolonial societies to the point that no intraspecific aggressiveness between workers was noted in different geographical areas of Australia over 3000 km (Fournier et al., 2009). Consequently, *P. megacephala* outcompetes native ants through interference competition and especially by raiding their colonies (Figure 1), a characteristic inherited from its native range that even permits it to resist the assault of army ants (Dejean et al., 2008, 2014; Dejean, Kenne, et al., 2007; Dejean, Moreau, et al., 2007; Sarnat et al., 2015; see Kamaru et al., 2024 for an indirect effect).

Unlike most other invasive ants, the red imported fire ant, *Solenopsis invicta*, is monogynous. Native to South America, it was imported into the United States in the 1930s around Mobile, Alabama. However, polygynous populations were found in Mississippi in 1973 that differed by the "social chromosome" regulating the social form; the smaller queens of the polygynous form can reproduce and spread through budding. Although the monogynous form is dominant in the United States, both forms can participate in mating flights (Arsenault et al., 2020; Kjeldgaard et al., 2022; Tschinkel, 2013). Colonies are omnivorous like other invasive ants and consume sugary food, mostly the honeydew of hemipterans. They also scavenge rather than being predatory and displace other ants through competition. Finally, it is considered one of the most costly invasive species worldwide, impacting natural ecosystems, agriculture, man-made structures, and human health (Chen et al., 2020; Menchetti et al., 2023; Tschinkel, 2013).

In Florida, USA, the prevalence of both *P. megacephala* and *S. invicta* populations in certain invaded habitats makes it likely that these two dominant and invasive species encounter each other regularly (see Booher et al., 2023), but the nature of their interactions has not been clarified. Knowledge about such interactions could elucidate how

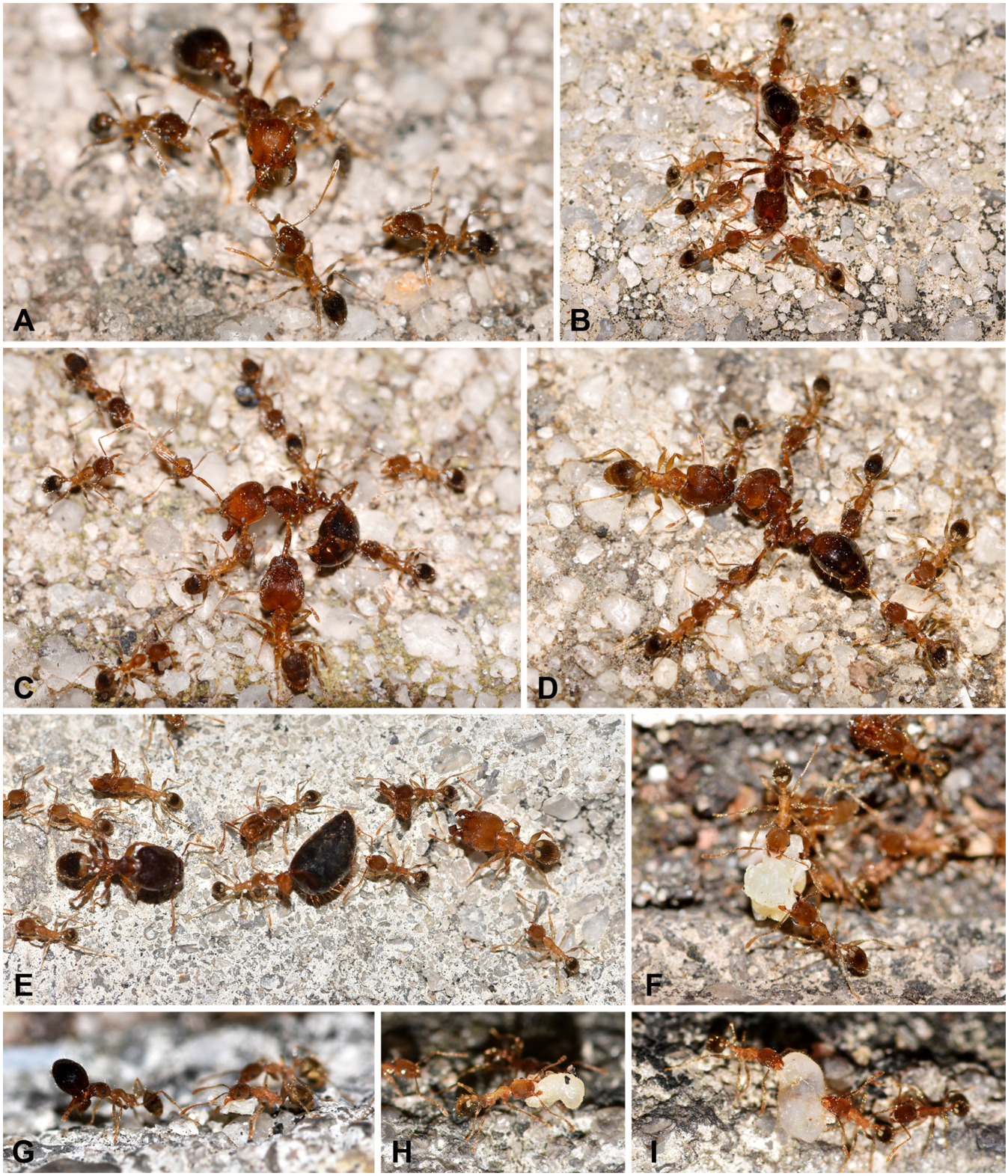


**FIGURE 1** Sequence of the capture of *Solenopsis invicta* workers by *Pheidole megacephala*. (A) *P. megacephala* minors begin to attack a large *S. invicta* worker. (B) Nine *P. megacephala* minors spread-eagle an *S. invicta* worker. (C) A *P. megacephala* soldier is cutting off the last intact leg of an *S. invicta* worker that is trying to sting it. (D) A *P. megacephala* minor seizes the stinger of a dismembered *S. invicta* worker. (E) After the raid, *P. megacephala* workers retrieve pieces of *S. invicta* workers, including a large gaster. (F–I) *P. megacephala* workers retrieving *S. invicta* pupae and larvae at the end of a raid (Photos: Airlan San Juan).

dominant invasive species co-exist and partition an environment.

The area studied is in a highly disturbed suburban environment located in the town center of a gated community in Poinciana, Florida. This area and its surroundings are overrun by several invasive species, including *P. megacephala*, *Pheidole* sp. cf. *parva*, and *S. invicta*. Ant specimens were placed in 91% isopropyl alcohol for later identification by Douglas B. Booher (USDA Forest Service, Southern Research Station, Athens, GA 30602, USA). DNA was extracted for the identification of *Pheidole* sp. cf. *parva*, which is new to the area.

To determine the precise territory occupied by *P. megacephala*, we first located typical nest mounds or the semi-permanent trail networks of the species (see fig. 10 in Warner & Scheffrahn, 2007). Then, we placed baits (cookie crumbs, honey, and pieces of sausage) every 1–5 m to have an idea of the possible dimensions of the colony's territory. Finally, we transferred *P. megacephala* workers from the farthest points of the territory to confirm that they belonged to the same colony. Indeed, all transferred workers were accepted by resident individuals and generally followed the same paths and/or entered new nests unharmed. This territory covered an irregular area of two hectares, with the majority of the nest entrances situated along the town center's Village Drive (Appendix S1: Figure S1 on which we also noted the location of *S. invicta* mounds).

Aggressive interactions involving the *P. megacephala* colony and other ant species were noted during daily observations extending from June to November 2024. Special attention was paid to the periphery of the colony where contact between *P. megacephala* workers and other ant species was most common. Details of these interactions are described below.

When a single *P. megacephala* worker meets an allospecific ant, it seizes one appendage and drags the ant back toward its nestmates. Due to their large numbers and their ability to recruit at short and long ranges, in a well-coordinated effort, each worker seizes the appendages of the prey ant and pulls backward, spread-eagling it. This behavior is possible as, up to a certain point, *P. megacephala* workers are not affected by the venom sprayed by formicine ants such as *Camponotus* (mostly formic acid) or deposited on their cuticle via the stinger by myrmicine ants, including *S. invicta* (contains piperidine alkaloids). Then, recruited *P. megacephala* soldiers use their powerful mandibles to rapidly kill the prey, cutting off its legs and antennae, removing its gaster, or decapitating it (Figure 1, Appendix S1: Figure S2, Video S1). This process of immobilizing and killing prey occurred in all of the following four situations.

1. For an unknown reason, a column of *S. invicta* entered the *P. megacephala* territory. Although numerous, the *S. invicta* intruders acted individually, using their mandibles and stinger to kill some *P. megacephala* minor workers and soldiers that tried to defend the area during one-on-one fights, but they never retrieved them as prey. Meanwhile, *P. megacephala* recruited at long range numerous nestmates and was able to capture, kill, and retrieve some *S. invicta* workers and ultimately drive them out of their territory.
2. We placed baits around the periphery of the *P. megacephala* colony. Three possible scenarios unfolded depending on the persistence of the combat-ants. (1) Workers of the very agile and opportunistic formicines *Brachymyrmex obscurior* and *Paratrechina longicornis* rapidly left the bait when confronted with *P. megacephala*, although a few of these fleeing ants were captured (occurred frequently; >10 cases each). (2) Similarly, when the mass-recruiting *Pheidole* sp. cf. *parva* abandoned the baits as *P. megacephala* workers approached, combats were rare and fewer ants were killed (less than five deaths, mostly soldiers; more than 10 cases). If the *Pheidole* sp. cf. *parva* retreated only after trying to resist the attack, *P. megacephala* followed them back to their nest, forced these smaller ants to abscond, and plundered their brood (three cases). (3) When *S. invicta* contested baits with *P. megacephala*, the outcome depended on the ability of each species to deploy sufficient numbers of workers and soldiers to protect the bait. If *S. invicta* foragers persisted in trying to break through a cordon of *P. megacephala* that already dominated the bait zone, usually more than 10 *S. invicta* workers were spread-eagled, killed, and retrieved each time, and the remaining individuals abandoned the bait. Yet, in one out of the seven cases, an impressive force of *P. megacephala* drove *S. invicta* foragers away from the bait with no casualties on either side.
3. *P. megacephala* individuals encountered the foraging trail of another ant species. (1) After discovering a foraging trail of *S. invicta*, *P. megacephala* workers recruited nestmates at short and long ranges. They attacked, spread-eagled, and killed numerous workers and then transported them back to their nest. The attack lasted the entire night and disrupted the *S. invicta* foraging trail (one case). (2) When *P. megacephala* individuals encountered the foraging trails of *Camponotus floridanus*, these very large formicine workers bit or sprayed their venom and escaped the attacking *P. megacephala*. However, the *P. megacephala* minors were sometimes able to seize the legs of a *Camponotus* worker and slow it down long

enough for it to be immobilized, spread-eagled, killed, and retrieved (four cases).

4. Finally, *P. megacephala* can expand their territory by raiding the nests of other ant species and destroying entire colonies or causing them to abscond. Some raids are the end result of conflict at baits when the *P. megacephala* workers follow retreating alien ants and try to enter their nest. Successful raids start with the *P. megacephala* preying first on the adult ants defending the nest before capturing queens, alates, callow workers, pupae, and larvae. This was observed for three competing species. (1) For a *Crematogaster* sp. colony that nested close to the *P. megacephala* border, the raid occurred overnight and resulted in the disappearance of the colony by the following day. (2) By contrast, raids on *Pheidole* sp. cf. *parva* colonies occurred multiple times due to the numerous nests of this species in the area. Soldiers and workers that resisted were killed, permitting *P. megacephala* individuals to plunder their nests, retrieving the larvae and pupae (seven cases). (3) The same situation occurred for *S. invicta* that was raided over more than 24 h (two cases from different areas, but *S. invicta* colonies can be huge). Here, too, numerous defending *S. invicta* workers were killed and retrieved as prey, along with many larvae, pupae, and a dealated queen (Video S1). By absconding rapidly during a third encounter, *S. invicta* avoided losing many workers. The *S. invicta* workers ran frantically around the nest entrance before piling up eggs, larvae, and pupae and carrying them away. A fourth *S. invicta* colony clashed with *P. megacephala* twice at baits, losing more than 10 workers each time, before being raided overnight and absconding. Finally, in each of these four situations, the *P. megacephala* occupied the *S. invicta* nest and then consolidated control over the area during the following weeks (synthesis in Figure 2).

In Florida, *P. megacephala* populations increased between 1965 and 2018 (see fig. S2 in Booher et al., 2023), but concerning the size of the colonies' territory, we can only assert that there is no intraspecific aggressiveness between workers over 2 ha. Because we know that in Australia no aggressiveness was noted over 3000 km (Fournier et al., 2009), complementary studies are needed to determine more precisely the size of their territories. However, we noted here that the colony studied is large enough to raid small ant colonies, confirming previous results (Dejean et al., 2008; Dejean, Kenne, et al., 2007), as well as the large *S. invicta* colonies, themselves invasive. We cannot exclude the possibility that, due to their large size, *S. invicta* colonies can limit the impact of these raids underground by sealing galleries, a method employed by the invasive subterranean Formosan termite, which is able to limit *P. megacephala*'s preying activity (Chouvenc et al., 2015). Thus, further studies are needed to verify whether *P. megacephala* is able to destroy entire *S. invicta* colonies by raiding them.

In conclusion, for a predatory ant that raids other ant species, the larger the prey colony, the more profitable the raid. If by doing so the predator also extends its territory, as noted here, both predation and territoriality are involved. Rather than "interference competition," this most closely resembles "intraguild predation" because the predator gains an energetic reward while reducing competition for space. Indeed, the two main species

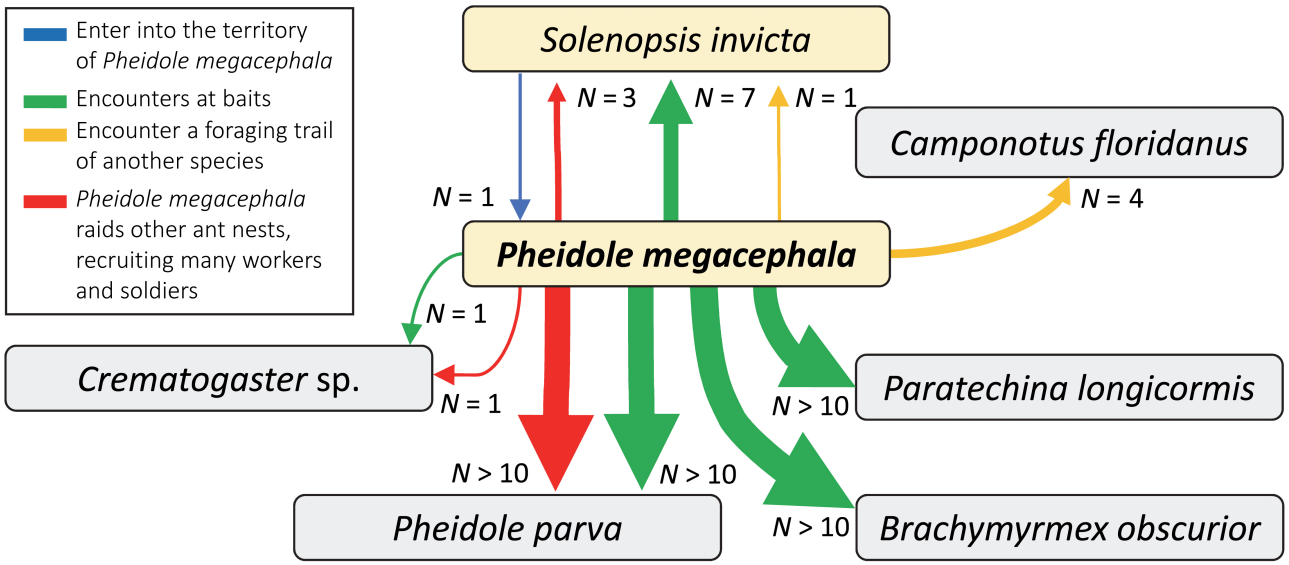


**FIGURE 2** Representation of the different types of encounters between *Pheidole megacephala* and other ant species, including *Solenopsis invicta* in the area studied in Poinciana, Florida, USA.

involved in this study belong to the same guild (large, omnivorous, ground-dwelling territorial colonies). *S. invicta* is a poor predator, while *P. megacephala* is one of the most effective ant predators as it is able to prey on other ants whatever their size and their venom composition, especially when its colonies reach a certain size.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Azémar et al., 2024) are available on Figshare at https://doi.org/10.6084/m9.figshare.27179934.

## ORCID

*Alain Dejean* https://orcid.org/0000-0002-3561-2248

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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