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SHORT COMMUNICATION

Specialized predation on *Wasmannia auropunctata* by the army ant species *Neivamyrmex compressinodis*

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Abstract: We report here the first case of an efficient and specialized predator of the invasive ant species *Wasmannia auropunctata*: the army ant *Neivamyrmex compressinodis*. Our results are based on a study that we conducted in French Guiana, a part of the *Wasmannia*'s native range. When *N. compressinodis* workers attacked *W. auropunctata* nests, the assaulted workers panicked and left the nests, some of them carrying brood. Nevertheless, during its raids on *W. auropunctata*, *N. compressinodis* was able to capture nearly all of the *W. auropunctata* brood and winged sexuals, whereas none of the attacks by *N. compressinodis* on other sympatric ant species were successful. Laboratory experiments revealed that the workers of eight compared sympatric species attacked the *N. compressinodis* individuals and that *N. compressinodis* workers accepted *W. auropunctata* brood as well as that of most of the tested species, showing that its specificity probably depends on the reaction of the *W. auropunctata* workers.

Key words: army ants, invasive ants, natural enemy, predation

1 Introduction

Several ant species that can proliferate quickly upon introduction into new areas are among the most devastating invaders known, as invasions by these ants often have major ecological consequences. *Wasmannia auropunctata*, a Neotropical myrmicine ant, has been dispersed through commercial activity throughout the tropics and is considered to be one of the most destructive of the invasive ant species (Holway et al. 2002; Wetterer and Porter 2003; Le Breton et al. 2004, 2005). In undisturbed areas in French Guiana, a part of their native range, *W. auropunctata* colonies can be found along the banks of streams where they reproduce sexually; however, in disturbed areas of their native range and in new areas where they have been introduced, they reproduce clonally and are abundant (Fournier et al. 2005; Le Breton et al. 2006).

Identifying the factors that regulate invasive ant populations in their native ranges constitutes a central key to understanding their success in introduced areas (Holway et al. 2002). In the case of *W. auropunctata*, only a few parasites and predators that may limit its proliferation in its native range have been identified; for example, eucharitid wasps of the genus *Orasema* specifically parasitize *W. auropunctata* (Heraty 1994). We do know, however, that New World army ants, or Ecitonianae, play a major role in the regulation of ground-dwelling insect populations, particularly other ants (Wheeler 1910; Droual 1983; Franks and Bossert 1983; Rettenmeyer et al. 1983; Gotwald 1995). Several ecitonine species are assumed to be specific predators of ants, some of them to the point of specializing in a particular genus or species (Perfecto 1992; LaPolla et al. 2002; Powell and Clark 2004). Workers of the army ant *Neivamyrmex pilosus* have been observed in Panama carrying off *W. auropunctata* brood (Tennant 1994).

We report here on *Neivamyrmex compressinodis*, a previously unrecognized natural enemy predator of *W. auropunctata* in its native range where we examined whether this army ant species is specialized in raiding *W. auropunctata* colonies.

2 Materials and Methods

Wasmannia auropunctata colonies are polydomous (multiple nests) and polygynous (multiple queens), and are very opportunistic in their nesting habits, exploiting an extremely broad array of superficial cavities situated under rocks, logs, leaf litter, epiphytes and those furnished by ant-plants (Wetterer and Porter 2003). *Neivamyrmex compressinodis*, an army ant originally described in Costa Rica, has rarely been sampled, thus its natural history remains unknown (G. Snelling, unpublished results). Along with several other species of this genus, workers range in size from 2 to 3 mm, and so slightly larger than *W. auropunctata* workers. Because most army ant species forage hypogaeically, it is rare to observe their attacks on litter- and ground-dwelling ants (but see Perfecto 1992; LaPolla et al. 2002; Powell and Clark 2004). We first noted raiding colonies of *N. compressinodis* in the forest edge situated at Petit Saut, French Guiana (5°04′N, 53°03′W). We then observed columns of this army ant species in the forest 12 times, but were able to locate the colony only once. After observing it in the field, we harvested that entire colony and found that the principal chamber was buried 30-40 cm deep and contained one queen, several thousand workers and a large quantity of brood. We installed this colony in an open, plastic box (30 × 30 cm) containing humidified dirt, itself placed inside of a 50 × 40 cm arena whose walls were coated with fluon® (Asahi Glass Co. LTD, Tokyo, Japan) to prevent the workers from escaping. The ants rapidly built a nest in the dirt and foraged in the arena.

We conducted experiments during 3 weeks using the colonies of nine sympatric ant species, including *W. auropunctata*, selected from among the most frequent in an area where *N. compressinodis* had also been noted (table 1). Each newly-harvested colony was installed in an artificial nest, a glass tube equipped with a watering place, permitting direct observation. Each nest was placed into an arena (50 × 40 cm; its walls coated with fluon®) connected by a bridge to the *N. compressinodis* hunting arena. Immediately after its installation, the *N. compressinodis* workers crossed the bridge and explored the adjacent box. We recorded the behaviour of the workers from each species tested during their encounters with *N. compressinodis* workers, paying particular attention as to whether their reactions were 'defensive' or 'panicked', and we noted if the first attacking *N. compressinodis* workers triggered mass recruitment. Another experiment consisted of using only the brood of some of the previously tested ant species.

3 Results

In the field, the 12 foraging *N. compressinodis* columns noted were most often observed under the leaf litter searching for other ant species, although workers can patrol on the ground or more rarely on low vegetation. In all cases, we noted that they preyed only on *W. auropunctata* colonies. Overall, we observed *N. compressinodis* successfully attack parts of more than 100 *W. auropunctata* colonies, whereas a similar number of sympatric ant colonies was ignored or avoided.

When encountering *W. auropunctata* individuals the *N. compressinodis* workers were visibly excited in a way not observed for any other ant encounters, and in all cases the *W. auropunctata* workers evacuated the attacked nests, most of them carrying brood. They then hid in the area, and later progressively returned to their nests transporting their saved brood. The *Neivamyrmex* raiders carried larvae, pupae and even winged individuals out of the nests, but the queens were spared. The raids ended when no brood remained in the nests (we verified afterwards). Based on our qualitative observations, the quantity of brood saved by *W. auropunctata* workers was considerably inferior to that retrieved by *N. compressinodis* raiders.

In laboratory experiments some *N. compressinodis* scout workers discovering a *W. auropunctata* nest were attacked and sometimes killed by the guards. Nevertheless, when the first *Neivamyrmex* individual did succeed in entering a nest, its presence immediately triggered panic in all *W. auropunctata* individuals that then evacuated the nest without showing any aggressive behaviour towards the raiding ants. Contrary to the workers, *W. auropunctata* queens remained immobile in the nests, and when antennated by *N. compressinodis* workers, they curled into a pupal posture and were never attacked, whereas winged females were killed and retrieved. By counting the ratio between the quantity of brood (number of larvae and pupae) and the number of workers, we estimated that *W. auropunctata* workers saved less than 15% of their brood from the attacking *N. compressinodis*, as only some workers were able to save only one larva or one pupa.

During their encounters with all other tested ant species *N. compressinodis* workers at the front of the columns attacked first, but the workers from the tested species counterattacked. They repelled the *N. compressinodis* individuals, defending the access to their nest by recruiting major workers (*Pheidole* spp.), using venom (*Crematogaster limata*), spraying formic acid (*Brachymyrmex* sp.) or by blocking the nest entrance (comparatively large workers of *Pseudomyrmex tenuis* and *Anochetus horridus*). The *N. compressinodis* workers ceased their attacks after a few minutes. In the second experiment, except for the case of *C. limata*, the *Neivamyrmex* workers raided the brood of *W. auro-*

Table 1. *Predation success of columns of* Neivamyrmex compressinodis *foragers on entire colonies or only the brood of various sympatric ant species. Corresponds to brood that were not tested*

Ant species tested	Entire colonies: Mass recruitment	Entire colonies: Predation success	Brood only: Brood acceptance	Brood only: Mass recruitment	No. cases
Wasmannia auropunctata	Yes	Yes	Yes	Yes	10
Anochetus horridus	No	No	–	–	4
Brachymyrmex sp.	No	No	Yes	Yes	6
Crematogaster limata	No	No	No	No	6
Cyphomyrmex rimosus	No	No	–	–	6
Paratrechina sp.	No	No	–	–	6
Pheidole radoskowskii	No	No	Yes	Yes	4
Pheidole fallax	No	No	Yes	Yes	6
Pseudomyrmex tenuis	No	No	Yes	Yes	4

punctata and that of the other tested ant species in the same way (table 1).

4 Discussion

The opportunistic nesting habits of *W. auropunctata* afford little protection from raids by army ants, but as the colonies are polydomous some nests are spared. The *W. auropunctata* workers evacuate their nests in a way similar to that noted for other ant species when raided by army ants: they leave their nest carrying brood (Droual 1983; Perfecto 1992; Gotwald 1995; LaPolla et al. 2002). Generally among adults only callow workers are attacked, but here winged males and females were also retrieved, whereas the queens were completely spared as has already been noted for other ecitonine raids (Franks and Bossert 1983; Rettenmeyer et al. 1983; Perfecto 1992; LaPolla et al. 2002; Powell and Clark 2004). Although the *W. auropunctata* workers joined their queens with the part of the brood they saved, the initial colonies were greatly affected, particularly through the complete destruction of reproductive offspring.

The inability of *N. compressinodis* to enter the nests of other ant species both in the field and in the laboratory highlights the specificity of this species, at least in the area studied. Nevertheless, this specificity is related only to the reactions of the *W. auropunctata* workers when confronted with *N. compressinodis* individuals because: (1) the workers of the other tested ant species not only did not panic, they even counter-attacked; and (2) *N. compressinodis* workers accepted the brood of most of the other tested species.

Our results have implications for understanding why *W. auropunctata* does not proliferate in its native range, even in pioneer areas where colonies reproduce clonally, and, thus, are relatively frequent. *Wasmannia auropunctata* colonies, like other litter-dwelling ants, are under the constant pressure of several army ant species whose high densities result in a steady and high rate of raiding (Kaspari and O'Donnell 2003). This pressure is all the more accentuated for *W. auropunctata* colonies because they are faced with a specific and particularly effective predator among these raiding ants, *N. compressinodis*.

The Lanchester theory of combat was proposed as a theoretical framework for explaining fighting between ants (Franks and Partridge 1993). The Linear law predicts that fighting ability contributes more towards victory than the number of combatants when a restricted area of combat forces individuals to engage in a series of duels, while the Square law predicts that when combatants can mix freely, numerical superiority is the deciding factor. A two-stage strategy where both Linear and Square laws come into play was shown when *Atta* spp. were attacked by their specialized predator *Nomamyrmex esenbeckii* (Powell and Clark 2004).

Our study shows that when it raids *W. auropunctata* nests, *N. compressinodis* does not even have to fight, or only rarely, because it releases an allomone that triggers panic among the *W. auropunctata* workers. This is a good example of the Linear law because it demonstrates how the emission of an allomone indirectly augments the force of the emitting workers, even when they are outnumbered, as noted for in slave-making ants (Franks and Partridge 1993) that emit propaganda allomones produced by the Dufour's gland (Lenoir et al. 2001; Brandt et al. 2006).

In conclusion, to the best of our knowledge, we have identified in this study the first specialized predator of *W. auropunctata*. The potential of using *N. compressinoides* to control introduced populations of *W. auropunctata* would require extensive studies as such introductions can turn out to be both good ideas and huge ecological mistakes. A potentially more fruitful application of our research findings may evolve via further investigation of the Dufour's gland and the chemicals used by *N. compressinodis* to induce panic in *W. auropunctata*.

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