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Cooperative self-defence: Matabele ants (*Pachycondyla analis*) against African driver ants (*Dorylus* sp.; Hymenoptera: Formicidae)

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Abstract

Only few documented cases of cooperative self-defence outside the nest are known in social insects. We report observations of *Pachycondyla analis* (LATREILLE, 1802) workers helping each other against attacking epigaeic driver ants (*Dorylus* sp.) in a West African savannah. The considerably larger *P. analis* scanned each other's legs and antennae and removed *Dorylus* clinging to their extremities. In experimentally staged encounters we could reproduce this behaviour.

Key words: Altruism, interspecific interaction, Ivory Coast, social insects.

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Introduction

Worker ants exhibit a wide range of complex cooperative behaviours. Examples include trophallaxis, which is almost ubiquitous in ants, cooperative foraging and food transport, and nest construction (HÖLLDOBLER & WILSON 1990). While cooperative nest defence is well known (HÖLLDOBLER & WILSON 1990), the cooperative "self-defence" of workers outside of the nest is less often observed. One of the rare documented cases of such behaviour is the leaf-cutter ant *Atta cephalotes* (LINNAEUS, 1758), where highly specialised minima workers protect larger workers from parasitic flies (FEENER & MOSS 1990, FEENER & BROWN 1993). In this note we report observations of cooperative self-defence among workers of the African ponerine ant *Pachycondyla* (*Megaponera*) *analis* (LATREILLE, 1802) when attacked by driver ants, *Dorylus* (*Anomma*) sp.

Methods and Material

Pachycondyla analis is a large ant species living in medium sized colonies of up to c. 600 workers (HÖLLDOBLER & WILSON 1990). The species is generally considered as dimorphic (majors' body length about 15 mm, minors': 9 - 11 mm; LONGHURST & HOWSE 1979, reviewed in TAYLOR 2006). *Pachycondyla analis* is a specialised termitophagous ant. Major "scouts" recruit troops of a dozen to several hundred workers via scent trails to the soil covers of foraging termites (e.g., *Macrotermes*, *Odontotermes*). Minors capture the termites inside these soil covers, and majors carry them back to *P. analis* nests over distances of up to 40 m (HÖLLDOBLER & al. 1994, BAYLISS & FIELDLING 2002, TAYLOR 2006).

Epigaeic West-African driver ants are commonly referred to as *Dorylus* (*Anomma*) *nigricans* ILLIGER, 1802, but as there is considerable taxonomic confusion whether workers really are conspecific with the single male specimen described by Illiger (e.g., RAIGNIER & VAN BOVEN 1955; reviewed in TAYLOR 2006) we refer to these ants as *Dorylus* sp. throughout this article. They live in extremely large colonies of up to several million workers (GOTWALD 1995). These small to medium-sized (own measurement of 17 individuals: median 6 mm, range 3 - 10 mm), blind ants forage by "flooding" areas of leaf litter or trees (including other ant or termite nests), attacking all prey within reach. Their vast numbers enable them to kill prey of a much larger size than their own (GOTWALD 1995). Complex behaviours and orientation of *Dorylus* swarms probably arise from self-organising mechanisms based on the interplay of relatively simple behavioural repertoires of individual ants (cf. FRANKS 1989 for Neotropical army ants). *Dorylus* sp. workers are very aggressive when disturbed along their foraging trails (up to 100 m long), which results in swarming and attacking anything within a radius of several meters. It is not clear if this aggressiveness provides protection against potential predators or if it is simply a type of foraging behaviour. Established foraging trails are usually buried, covered, or otherwise protected (GOTWALD 1995).

Both ant species are commonly seen in sub-Saharan West Africa. Observations and experiments reported here were carried out in November 1999 during a visit to Comoé National Park in northern Ivory Coast (08°30' - 09°36' N, 03°07' - 04°25' W). Vouchers of both taxa were deposited at the Natural History Museum Vienna.

Results and Discussion

We observed a *P. analis* foraging troop of about 60 individuals crossing a *Dorylus* sp. trail. When the driver ants

responded by attacking the legs and antennae of the "invaders", the much larger *P. analis* workers were capable of defending themselves by means of their sting and large mandibles. However, they frequently could not reach the *Dorylus* sp. workers clinging to their extremities, which considerably reduced their mobility (a commonly observed strategy of *Dorylus* sp. to overcome large prey). In these cases, other *P. analis* individuals helped their nestmates by scanning the victim's extremities and removing the driver ants' thorax and abdomen, often leaving *Dorylus* sp. heads with jaws still firmly locked on *P. analis*' extremities. In most manoeuvres of this kind "helpers" and "victims" were located next to each other prior to the behaviour, but in some instances we observed helpers to turn back from their initial running direction for up to c. 15 cm to rescue their nestmates.

To confirm and further investigate this observation we experimentally provoked conflicts between the two species. In three separate instances we collected about 40 *P. analis* workers from foraging troops, stored them in a PVC box, and transferred them to the nearest known *Dorylus* sp. trail. They were released close enough to *Dorylus* sp. to "accidentally" cross their trail. Although *P. analis* became strongly disorientated during these experiments (presumably due to the absence of their pheromone trail, cf. HÖLLDOBLER & al. 1994), we observed the reported behaviour several times in each experiment (see photograph in the Appendix, as digital supplementary material to this article, at the journal's web pages). However, not all attempts to remove *Dorylus* sp. were successful, and some *P. analis* were ignored by their nestmates and subdued by *Dorylus*. Performance might, however, have been weakened due to the state of confusion mentioned above. It is unclear if endangered workers can signal for help if necessary (e.g., by alarm pheromones), or if the behaviour is initiated by the helping individuals. In contrast to *Atta cephalotes* (see above), we did not observe any obvious caste specialisation with regard to this defence behaviour.

The cooperative "altruistic" behaviour we observed in *P. analis* is surprising as there are few reports of direct, costly interaction between worker ants except for trophallaxis. *Dorylus* sp. will always strongly outnumber *P. analis* troops in such encounters (which might not be uncommon, given the abundance of both species in the habitat), so a quick retreat with as few losses as possible should be the best behaviour in terms of the colony energy budget for *P. analis* (HÖLLDOBLER & WILSON 1990). We propose two possible scenarios for the evolutionary basis of this behaviour. It has been observed that *P. analis* workers also help each other to remove thorax markings (applied for research purposes) from their bodies (M. Stüben, pers. comm.). Therefore, the origin of the observed behaviour could be a pre-adaptation for cleaning and grooming. If, however, cooperative defence represents a specific adaptation, it remains to be investigated what specific ecological circumstances favoured the evolution of a behaviour that otherwise appears to be rarely observed in ants.

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Zusammenfassung

Unter sozialen Insekten sind nur wenige Fälle kooperativer Selbstverteidigung außerhalb des Nestes dokumentiert. Wir beschreiben hier Beobachtungen an *Pachycondyla analis* (LATREILLE, 1802)-Arbeiterinnen, die sich in einer westafrikanischen Savannenlandschaft gegen angreifende epigäische Treiberameisen (*Dorylus* sp.) verteidigten. Die deutlich größeren *P. analis* untersuchten einander gegenseitig Beine und Antennen, um *Dorylus*, die sich dort verbissen hatten, zu entfernen. In experimentell herbeigeführten Konflikten zwischen den beiden Arten konnten wir dieses Verhalten replizieren.

References

BAYLISS, J. & FIELDLING, A. 2002: Termitophagous foraging by *Pachycondyla analis* (Formicidae, Ponerinae) in a Tanzanian coastal dry forest. – Sociobiology 39: 103-122.

FEENER, D.H., JR. & BROWN, B.V. 1993: Oviposition behavior of an ant-parasitizing fly, *Neodohrniphora curvineris* (Diptera: Phoridae), and defence behavior by its leaf-cutting ant host *Atta cephalotes* (Hymenoptera: Formicidae). − Journal of Insect Behavior 6: 675-688.

FEENER, D.H., JR. & MOSS, K.A.G. 1990: Defence against parasites by hitchhikers in leaf-cutting ants: a quantitative assessment. − Behavioral Ecology and Sociobiology 26: 17-29.

FRANKS, N.R. 1989: Army ants: a collective intelligence. − American Scientist 77: 138-145.

GOTWALD, W.H., Jr. 1995: Army ants – the biology of social predation. − Comstock Publishing Associates & Cornell University Press, Ithaca, 302 pp.

HÖLLDOBLER, B., BRAUN, U., GRONENBERG, W., KIRCHNER, W. H. & PEETERS, C. 1994: Trail communication in the ant *Megaponera foetens* (FABR.) (Formicidae, Ponerinae). − Journal of Insect Physiology 40: 585-593.

HÖLLDOBLER, B. & WILSON, E.O. 1990: The ants. − Springer Verlag, Berlin, 733 pp.

LONGHURST, C. & HOWSE, P.E. 1979: Foraging, recruitment and emigration in *Megaponera foetens* (FAB.) (Hymenoptera: Formicidae) from the Nigerian Guinea savanna. − Insectes Sociaux 26: 204-215.

RAIGNIER, A. & VAN BOVEN, J. 1955: Étude taxonomique, biologique et biométrique des *Dorylus* du sous-genre *Anomma* (Hymenoptera: Formicidae). − Annales du Musée Royal du Congo Belge, n.s. 4 (sciences zoologiques) 2: 1-359.

TAYLOR, B. 2006: The ants of (sub-Saharan) Africa. − <http://antbase.org/ants/africa/>, retrieved on 30 May 2007.