



HAL
open science

Predation on large millipedes and self-assembling chains in *Leptogenys* ants from Cambodia

Christian Peeters, Stéphane de Greef

► To cite this version:

Christian Peeters, Stéphane de Greef. Predation on large millipedes and self-assembling chains in *Leptogenys* ants from Cambodia. *Insectes Sociaux*, 2015, 62, pp.471-477. 10.1007/s00040-015-0426-2. hal-02177049

HAL Id: hal-02177049

<https://cnrs.hal.science/hal-02177049>

Submitted on 19 Feb 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Predation on large millipedes and self-assembling chains in *Leptogenys* ants from Cambodia

C. Peeters¹ · S. De Greef²

Received: 26 May 2015 / Revised: 6 July 2015 / Accepted: 19 July 2015 / Published online: 8 August 2015
© International Union for the Study of Social Insects (IUSSI) 2015

Abstract Various ants can link their bodies in chains or other structures, a striking example of cooperation. Chain behavior in *Leptogenys* sp. functions for the collective transport of large millipedes. This undescribed *Leptogenys* species is a swarm raider with a small range of prey: millipedes belonging to four orders (Polydesmida, Spirostreptida, Spirobolida, Sphaerotheriida), and occasional earthworms. Small prey were carried individually or dragged by a few ants, while chains made it possible to move millipedes weighing up to 16.4 g. Chains (either linear or branched) changed according to obstacles along the way to the nests. Between 2 and 52 workers were observed to drag single prey items, with only a few ants directly grasping the prey. One 15-cm-long millipede was captured rodeo-style after being encircled by 25–30 ants. As it uncurled from a defensive coil, the ants held back except one that tried to sting between its legs. The millipede started thrashing about which caused many ants to attempt stinging. While four other ponerine genera hunt millipedes solitarily, chains have never been reported.

Keywords Cooperative transport · Self-assemblages · Swarm raiding · Foraging · Ponerinae · Diplopods · Spirostreptida · Sphaerotheriida

Introduction

Self-assemblages are a spectacular example of cooperation among eusocial insects, with a variety of forms and functions. *Oecophylla* ants use pulling chains to bring leaves closer during nest construction, *Solenopsis* and others assemble rafts to survive flooding, army ants make bridges and ramps to facilitate mass movement (reviewed in Anderson et al. 2002). However, chains have never been reported in the context of predation. Videos of ant workers using long chains to drag big millipedes (“daisy chains”) were posted on the internet during 2014, attracting huge interest. This behavior appears restricted to SE Asia, and represents the first record of millipede predation in *Leptogenys*. Millipedes are among the best protected arthropods due to their articulated body armor and quick coiling response, as well as noxious defensive secretions (e.g., benzoquinones, hydrogen cyanide, terpenoids). Accordingly, millipede predation is rare in ants. A few Ponerinae hunt them solitarily, i.e., *Myopias julivora* (Willey and Brown 1983), *Probolomyrmex dammermani* (Ito 1998), all species of *Plectroctena* (Bolton 1974; Dejean et al. 2001) and *Thaumatomyrmex* (Brandão et al. 1991; Jahyny et al. 2008). Two species of *Gnamptogenys* (subfamily Ectatomminae) are also reported to hunt millipedes (Brown 1992; Longino 2015).

Strict carnivory is the hallmark of Ponerinae. Most species hunt alone but closely related species can be formidable group hunters (e.g., Peeters and Crewe 1987). Predation is either opportunistic or highly prey specific, and the latter

Electronic supplementary material The online version of this article (doi:10.1007/s00040-015-0426-2) contains supplementary material, which is available to authorized users.

✉ C. Peeters
christian.peeters@upmc.fr
S. De Greef
Stephane@stephanedegreef.com

¹ Institute of Ecology and Environmental Sciences, UMR CNRS 7618, Université Pierre et Marie Curie, 75005 Paris, France

² 24 avenue du Général De Gaulle, 17252 Siem Reap, Cambodia

characterizes many Ponerinae. *Leptogenys*, which make up a quarter of all Ponerinae (>300 species, distributed globally), are mostly strict prey specialists, e.g., terrestrial isopods (oniscoids), termites or earwigs (Bolton 1975; Dejean and Evraerts 1997; Lattke 2011; Schmidt and Shattuck 2014). We describe how *Leptogenys* sp. from Cambodia uses chains for the cooperative transport of large prey, and we provide natural history details.

Materials and methods

All our observations are field based, from two localities in Siem Reap province, Cambodia: Phnom Kulen National Park (June 2010) and Angkor Thom (September 2014). *Leptogenys* sp. is a large (14 mm), distinctly bluish species in the process of being described by Koichi Arimoto and Seiki Yamane. It seems closely related to *L. chalybaea* Emery from Borneo, but has stronger sculpture especially on gastral tergites. This new species of *Leptogenys* occurs in dipterocarp forests with a dense understory, and we selected cleared areas (e.g., along paths or grassy patches) for better viewing. Millipede hunting was only observed during the rainy season (end of June–October), and this may be linked to activity patterns of the millipedes. Behavioral sequences were recorded with videos and photos for subsequent detailed examination. Our data about prey retrieval involved three ant colonies. Life history information was also obtained.

Results

Millipede location

We observed several raiding parties consisting of 20–50 workers. Each worker was following the previous one in a single continuous line, traveling slowly. Some individuals drifted off and explored the periphery (Online video 1). It is not known if the ants can pick up the scent of potential prey, or if they encounter them by chance. On one occasion, an ant nest was located in the undergrowth, with cleaned-out millipede rings scattered around the entrance, and raiding parties of various sizes leaving and returning.

Millipede capture

We placed one large (15 cm-long), coiled up millipede (Order Spirostreptida, family Harpagophoridae, *?Thyropygus* sp.) on the ground 3 m ahead of a raiding party. A few workers approached carefully and briefly antennated its cuticle, then backed off 1–2 cm. Ants did not bite or sting the millipede at first contact. Within 1 min, 25–30 static workers surrounded the prey from all angles, facing towards

it (Fig. 1). When the millipede slowly uncoiled, the ants remained still for about 10 s as it began to walk away. One worker then tried to bite or sting the leg region of the front segments, which caused the millipede to withdraw violently and nearly stand on end. This triggered many workers to attack simultaneously and attempt stinging the vulnerable underside between the legs (Online video 2). As the millipede continued to wriggle vigorously and slide away on its back, only a few workers managed to hold on and sting. This rodeo-style behavior continued for more than 10 min as the millipede writhed intermittently, managing to dislodge some but not all of the attacking ants. Whenever the millipede moved away, dozens of ants ran after it and continued attacking. No injuries were seen, but several workers walked off cleaning legs and antennae, possibly to remove secretions from the prey.

Millipede retrieval

With the *Thyropygus* millipede struggling less and less (presumably paralyzed after many stings), the ants began to drag the prey (subsequent measurement indicated a fresh weight of 16.4 g., i.e., more than a thousand times the weight of an individual ant). Ants grasped several available points, i.e., antennae and legs. Chains formed in a few places, but the ones that persisted longer were anchored to the antennae. During self-assembly of these chains, a lead ant grabbed one appendage of the prey, then a second ant used her mandibles to grab the lead ant around the constriction between first and second gaster segments (Fig. 2). A third ant grabbed the second in the same way, and as a result a variable number of ants could pull the heavy prey without their leg movements impeded (Online video 3). Chains only occurred forward of the prey (i.e., always pulling, not pushing). Some chains were branched, bifurcating when two workers grabbed the same preceding ant, using both gaster and mid-thorax; such ant then became the



Fig. 1 Members of a swarming raid of *Leptogenys* sp. ready to attack a 15 cm-long millipede (order Spirostreptida, family Harpagophoridae, *?Thyropygus*) in a defensive coiled position. Photograph courtesy of S. De Greef © 2015



Fig. 2 A branched chain used to move the *Thyropygus* millipede. Three branches of 18, 15 and 19 workers are attached to a single worker grabbing the millipede's antenna (see Electronic

supplementary material). Note other workers grabbing legs on one side. Photographs courtesy of S. De Greef © 2015



Fig. 3 Details of linear chains (long or short) used to drag millipedes of different sizes **a** Harpagophoridae (*Thyropygus*), 16.4 g fresh weight; **b** Pachybolidae, 1.9 g fresh weight. Photographs courtesy of S. De Greef © 2015

junction of 2 or even 3 different chains, with up to 52 workers involved (Fig. 2). Two or three linear chains sometimes formed in parallel, attached to distinct parts of the prey. Sometimes the leading ant lost her grip, but the chain did not break up immediately, and it is unclear what information the participants use to know it has broken. The longest linear chain involved 20 workers (Fig. 3).

Chains broke and reformed frequently, especially when encountering obstacles (Online video 3). Moving large prey is harder over rough terrain covered with leaves and twigs. Several workers walked in front and appeared to clear a path by walking underneath objects and pushing up and down to widen the gaps. Millipedes slide easily when lying on their side, unhindered by the legs, while another *Thyropygus* was dragged on its back. Many workers grabbed legs of the prey, standing more or less perpendicular to the direction of movement (Fig. 2).

Other prey

Cooperative transport of a small variety of prey was observed (Table 1), indicating a marked preference for millipedes, although there is opportunism (earthworm, snail with a broken shell). In 3 days of observation, 1 *Thyropygus*, 1 Pachybolidae and 4 *Zephronia* were captured. Shorter chains were enough to

move smaller prey (Fig. 4, Online video 4), and a single ant carried a 15 mm-long millipede (Fig. 5a). Branched chains were only associated with big millipedes (Fig. 2), although some ants very briefly attached to existing linear chains.

Life history

Episodes of nest-moving were observed several times on 1 day, with numerous cocoons and larvae transported in a well defined file (similar to *L. nitida*, Duncan and Crewe (1994)). Emigrations followed the same trails as raiding parties, and the two events seem intricately connected. On one occasion, remains of millipedes (single segments, pairs of legs, head) were carried behind the ant brood, and even a freshly killed pill millipede was dragged. A photo taken of the emigration column crossing a dirt road allowed us to count over 250 workers, and colony size may reach 500–1000 workers.

Discussion

Cooperative transport, i.e., multiple individuals simultaneously moving an object, has evolved many times in ants, but is otherwise found mostly in humans (Czaczkes and

Table 1 Range of prey retrieved by *Leptogenys* sp. ants

Type of prey	Details of cooperative transport
Order Spirostreptida family Harpagophoridae <i>?Thyropygus</i> sp. #1	See text >100 ants in group. Linear and branched chains
<i>?Thyropygus</i> sp. #2 * 130 mm long	44 ants in group, rough terrain, 2 linear chains (6 and 2 ants), prey carried on back
Order Spirobolida, family Pachybolidae, red-legged millipede, 70 mm long, 1.9 g fresh (Fig. 3b)	20 ants in group, 10–14 do transport and others walk ahead. Prey is dragged by anal region with a short chain (4–5 ants), 3 single ants hold head region. After an obstacle, main chain grows to 6 ants, side chain has 2 ants, 10 ants bite other legs
Order Sphaerotheriida, family Zephroniidae, pill millipede (blue-legged), <i>Zephronia</i> sp. (Fig. 4), 15 mm long, curled up in a ball	Dragged in different ways: - flat sand: two chains of 3 ants, or a single chain of 6 ants - in grass, rough terrain: two chains (5 and 3 ants), dragging often stops and chains break
Pill millipede 15 mm long, not curled up (Fig. 5b)	Dragged by 3–4 ants: antenna (1 ant) and legs (2 ants). No chain, but sometimes a second ant grabs the gaster of worker grasping antenna. A few ants walk in front and a few more behind
Pill millipede 30 mm long, not curled up	Initial group of 10 ants, rough terrain. One chain of 5 ants anchored to an antenna, second chain of 3 ants on edge of first segment after head. More ants arrive, 7 ants grab legs. Later, one more chain of 2 ants on other antenna. Too much friction, prey stops sliding forward, chains break up. Within few seconds, two parallel chains (3 and 2 ants) start, and increase in length (up to 5 ants). Workers in front clear gaps
Pill millipede 10 mm long	Dragged by 10 workers, short-lived chain of 2 ants
Order Polydesmida, family Paradoxosomatidae, millipede 15 mm long (Fig. 5a)	No chain, carried by single worker
Snail with a damaged shell family Ariophantidae	Raiding party of \pm 50 ants, repeated stinging. 30 ants then leave while 20 remain. Small pieces of debris and twigs put on mucus-covered foot. Small parts cut and carried away by single ants
Earthworm 110 mm long	Group of 27 ants, one chain (3 ants)

Several of these sequences can be seen in Online video 4

* Observed in Phnom Kulen (June 2010)



Fig. 4 Short chains used to retrieve a pill millipede (*Zephronia* sp.) over smooth terrain. **a** A group of 15 ants walked ahead, another 10 ants followed. **b** Leading ant grasped the edge of body between head and anal region. Photographs courtesy of S. De Greef © 2015

Ratnieks 2013). Here, we document how workers in a new species of *Leptogenys* (near *chalybaea*) can assemble in chains to move heavy prey. Self-assembly occurs in various social insects (Anderson et al. 2002), but has not been recorded in the context of cooperative transport. Our non-manipulated observations indicate that *Leptogenys* sp. chains are dynamic, e.g., extra workers can join when obstacles impede movement of prey, thus requiring more force. Similarly, chains were shorter to move smaller

millipedes. Unlike the chains and ladders of *Eciton* and *Oecophylla* where participating individuals are motionless (discussed in Anderson et al. 2002), chain members in *Leptogenys* sp. must walk backwards and exert a pulling force. In general, the efforts of dozens of individuals are difficult to synchronize, and a few long chains may provide a “built-in” solution. Each chain is a vector of pull hence fewer and longer chains mean fewer and stronger vectors, and only 2–3 vectors need to be organized instead of

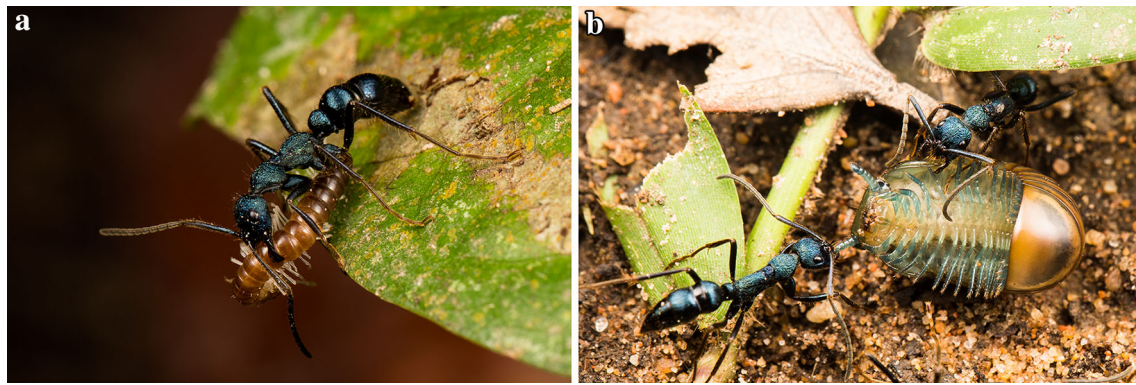


Fig. 5 Single foragers retrieving smaller millipedes: **a** order Polydesmida, family Paradoxosomatidae; **b** pill millipede, order Sphaerotheriida, family Zephroniidae, *Zephronia* sp. Photographs courtesy of S. De Greef © 2015

numerous workers. The involvement of additional workers on the millipede's underside is intriguing (Fig. 2): it is unclear if they are pulling or pushing forward. Experiments are needed to determine if these workers lift the prey to reduce friction with the ground, or exert a pulling force sideways. Sometimes such workers were the start of very short lateral chains (2–3 ants), hinting that an ant busy pulling stimulates other workers to grab its gaster, although this may not always contribute to the overall efficiency of prey retrieval. In addition to the workers assembled in chains or biting the millipede's legs, other members of a successful swarm raids walk freely in front, sides or at the back, hence available for contingencies.

Leptogenys shows a continuum of foraging behaviors, from solitary hunting and prey retrieval, to group hunting following recruitment of nestmates by a single forager ('scout'), to swarm raiding (Dejean and Evraerts 1997; Schmidt and Shattuck 2014). In *L. diminuta*, scouts trigger raids that can comprise up to 50 % of a colony's worker force, but only when large prey need to be subdued and retrieved (Witte et al. 2010). Other species have done away with scouts, instead engaging in swarm raids akin to those of true army ants. In *L. nitida*, 30–100 workers follow a pheromone trail (laid with the pygidial gland) and fan out at various intervals to search for prey (Duncan and Crewe 1994). Such swarm raids are very similar to *Leptogenys* sp. from Cambodia, although prey selection is completely opportunistic in *L. nitida* (most arthropods were attacked, but not millipedes).

Swarm raiding seems essential to capture large and mobile prey, but additional traits make *Leptogenys* sp. a highly specialized millipede predator. At the beginning of prey capture, single antennal contacts with a millipede were enough for many workers to behave in a highly restrained manner, leading to encirclement of the prey (Fig. 1). In *L. diminuta*, Witte et al. (2010) showed that scouts make decisions very quickly (i.e., recruit nestmates or not), and

that they can use surface chemicals to identify prey types. Similarly, we assume that *Leptogenys* sp. workers can recognize millipedes after antennating their exoskeleton (visual cues may be used to assess size), enabling a synchronous attack. Many ant stings are needed to prevent a large millipede from escaping, and stinging is only possible after it uncoils. The writhing millipede resists forcefully and for a long time, hence sufficient ants must follow it and continue stinging attempts. Ants must also withstand the defensive secretions produced along the flanks of the millipede's body; videos show that several ants started to groom during an attack. Only the first five segments, and the last, are devoid of defensive glands (Eisner et al. 1998).

Probolomyrmex dammermani (Indonesia; Ito 1998) and all species of *Thaumatomyrmex* (Brazil; Brandão et al. 1991) are specialized predators of polyxenid millipedes, which are armed with barbed bristles that need to be removed before eating. Single foragers are able to sting and immobilize such prey. In *Plectroctena* (Africa; Bolton 1974), single hunters can subdue and drag a millipede underneath their body (Fig. 6). The mandibles of *P. minor* are long enough to grip prey up to 4 mm in diameter (i.e., body 6–9 cm long, weighing 1.3–3.5 g), but larger millipedes escaped in 75 % of cases (Dejean et al. 2001). Single workers can move prey up to 100 times their own weight. When one worker cannot move an immobilized prey, it recruits two to five nestmates (Schatz et al. 2001). In *Myopias julivora* (Papua New Guinea; Willey and Brown 1983), abundant remains of millipedes were found in nest chambers, and the length and shape of ant mandibles is consistent with millipede predation. *Gnamptogenys ingeborgae* (Colombia; Brown 1992) hunts alone and favors polydesmid millipedes that are protected with cyanide compounds. In *Gnamptogenys bispinosa* (Costa Rica; Longino 2015), group raids have been observed but the ants retrieved millipedes with great difficulty, with a worker clinging to almost every legs, and certainly no chains.



Fig. 6 Forager of *Plectroctena mandibularis* (Ponerinae) single-handedly wrestling a millipede (unidentified), and carrying it back to its nest. © 1983 C. Peeters

In Thailand (e.g., Chonburi province), chains of *Leptogenys* ants (local name is ‘mod tanoy’) moving large millipedes are commonly seen in farmlands (N. Phansua pers. comm.). In Danum Valley, Borneo, an anonymous video shows that a different species of *Leptogenys* also uses very long chains to retrieve a large millipede. In Thailand, groups of *Leptogenys kitelli* can be seen retrieving large earthworms, but chains are not used (D. Wiwatwitaya pers. comm.). Heavy tubular prey (including caterpillars) can be moved when many workers bite appendages on all sides.

Cooperative transport is ecologically important because it increases the range of food available to a colony, however, there is extreme interspecific variation in its efficiency in ants (McCreery and Breed 2013). *Leptogenys* sp. are swarm raiders, hence many workers are available to assemble in longer chains as required by environmental context. Chain members walk backwards, so the end workers presumably follow chemical signals, and these may be emitted by the workers walking freely in front. No particular morphological adaptations are needed to form chains, although a sturdy exoskeleton and the marked constriction between first and second gaster segments (typical of Ponerinae) are probably prerequisites, allowing an effective mandible grip. We think that only large ponerine ants with a thick cuticle could survive rodeo-style capture of heavy and vigorous prey, and other ants would be crushed when a millipede thrashes about, hitting the ground with considerable force. Many species of *Leptogenys* with large workers occur in Africa and the Neotropics (Bolton 1975; Latke 2011), while large millipedes are also distributed on these continents. Yet chain behavior has never been reported outside SE Asia, suggesting that its evolution requires a complex combination of traits.

Supplemental videos

Short videos of millipede hunting and retrieval can be visioned at: <https://vimeo.com/album/3490590/>.

Acknowledgments We thank Sophany Phauk (Royal University, Phnom Penh) for support, Jean-Jacques Geoffroy (Muséum National d’Histoire Naturelle, Paris) and Sergei Golovatch (Russian Academy of Sciences, Moscow) for identification of millipedes, Seiki Yamane and Koichi Arimoto (Kyushu University, Fukuoka) for help with *Leptogenys* taxonomy, Adam Cronin, Tomer Czaczkes and Thibaud Monnin for useful comments. CP is funded by the French National Research Agency (ANTEVO ANR-12-JSV7-0003-01).

References

- Anderson C, Theraulaz G, Deneubourg J-L (2002) Self-assemblages in insect societies. *Insect Soc* 49:99–110
- Bolton B (1974) A revision of the Ponerine ant genus *Plectroctena* F. Smith (Hymenoptera: Formicidae). *Bull Br Mus (Nat Hist) Entomol* 30:309–338
- Bolton B (1975) A revision of the ant genus *Leptogenys* Roger (Hymenoptera: Formicidae) in the Ethiopian Region, with a review of the Malagasy species. *Bull Br Mus (Nat Hist) Entomol* 31:235–305
- Brandão CRF, Diniz JL, Tomotake EM (1991) *Thaumatomyrmex* strips millipedes for prey: a novel predatory behaviour in ants, and the first case of sympatry in the genus (Hymenoptera: Formicidae). *Insect Soc* 38:335–344
- Brown WL (1992) Two new species of *Gnamptogenys*, and an account of millipede predation by one of them. *Psyche* 99:275–290
- Czaczkes TJ, Ratnieks FL (2013) Cooperative transport in ants (Hymenoptera: Formicidae) and elsewhere. *Myrmec News* 18:1–11
- Dejean A, Evraerts C (1997) Predatory behavior in the genus *Leptogenys*: a comparative study. *J Insect Behav* 10:177–191
- Dejean A, Suzzoni JP, Schatz B (2001) Behavioral adaptations of an African ponerine ant in the capture of millipedes. *Behaviour* 138:981–996
- Duncan FD, Crewe RM (1994) Group hunting in a ponerine ant, *Leptogenys nitida* Smith. *Oecologia* 97:118–123
- Eisner T, Eisner M, Attygalle A, Deyrup M, Meinwald J (1998) Rendering the inedible edible: circumvention of a millipede’s chemical defense by a predaceous beetle larva (Phengodidae). *PNAS* 95:1108–1113
- Ito F (1998) Colony composition and specialized predation on millipedes in the enigmatic ponerine ant genus *Probolomyrmex* (Hymenoptera, Formicidae). *Insect Soc* 45:79–83
- Jahyny B, Lacau S, Delabie JHC, Fresneau D (2008) Le genre *Thaumatomyrmex* Mayr 1887, cryptique et prédateur spécialiste de Diplopoda Penicillata. In: Jiménez E, Fernández F, Arias TM,

- Lozano-Zambrano FH (eds) Sistemática, biogeografía y conservación de las hormigas cazadoras de Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, pp 329–346
- Lattke JE (2011) Revision of the New World species of the genus *Leptogenys* Roger (Insecta: Hymenoptera: Formicidae: Ponerinae). *Arthropod Syst Phylog* 69:127–264
- Longino J (2015) Ants of Costa Rica. <http://ants.biology.utah.edu/~longino/Genera/Gnamptogenys/SPECIES/bispinosa/bispinosa.html>. Accessed 29 March 2015
- McCreery HF, Breed MD (2013) Cooperative transport in ants: a review of proximate mechanisms. *Insect Soc* 61:99–110
- Peeters C, Crewe R (1987) Foraging and recruitment in ponerine ants: solitary hunting in the queenless *Ophthalmopone berthoudi* (Hymenoptera: Formicidae). *Psyche* 94:201–214
- Schatz B, Suzzoni JP, Corbara B, Dejean A (2001) Selection and capture of prey in the African ponerine ant *Plectroctena minor* (Hymenoptera: Formicidae). *Acta Oecol* 22:55–60
- Schmidt C, Shattuck S (2014) The higher classification of the ant subfamily Ponerinae (Hymenoptera: Formicidae), with a review of ponerine ecology and behavior. *Zootaxa* 3817:1–242
- Willey RB, Brown WL (1983) New species of the ant genus *Myopias* (Hymenoptera: Formicidae: Ponerinae). *Psyche* 90:249–286
- Witte V, Schliessmann D, Hashim R (2010) Attack or call for help? Rapid individual decisions in a group-hunting ant. *Behav Ecol* 21:1040–1047