

SHORT COMMUNICATION

Synchronized group retrieval of honeydew by *Prenolepis* ants in Singapore

CHRISTIAN PEETERS^{1*} AND GORDON YONG²

¹Institute of Ecology and Environmental Sciences, UMR CNRS 7618,
Sorbonne Universités UPMC, Paris 75005, France

²Department of Biological Sciences, National University of Singapore,
14 Science Drive 4, Singapore 117543

*Corresponding author: christian.peeters@upmc.fr

Keywords: foraging, repletes, temporal niche, Formicinae

Tropical forests show exceptionally high diversity of ant species. In Borneo, up to 717 species and 52 subspecies have been recorded (Pfeiffer et al. 2011). The numerous factors that account for niche separation are incompletely understood. Different ant species include predators, scavengers and herbivores (feeding on honeydew excreted by aphids and scale insects), and a great variety of foraging strategies are used (Lanan 2014). Moreover, a large range of body sizes means that the same lifestyles can be repeated multiple times at different scales (Peeters & Ito 2015). Another important factor are diel differences (24-hour period) in foraging activity among ant assemblages (Carroll & Janzen 1973, Yamane et al. 1996). In tropical rainforest on Borneo, baits on trunks were primarily occupied by ground ants during day-time, and arboreal ants at night (Hashimoto et al. 2010). Furthermore, ground ants preferred honey baits while arboreal ants preferred tuna baits, indicating that ground ants forage in the canopy to acquire carbohydrate nutrients, mostly during day-time (Hashimoto et al. 2010).

Prenolepis (subfamily Formicinae) are smallish ants (2.4–4.9 mm total length) that generally inhabit soil, leaf litter, and rotten wood on the ground (LaPolla et al. 2010, Williams & LaPolla 2016). Most species appear to be generalist omnivores and often gather honeydew. *Prenol-*

epis reaches its highest levels of species diversity in SE Asia and southern China. With the exception of *P. imparis* (a wide-ranging species found in North America; Wheeler 1930, Lynch et al. 1980, Tschinkel 1987), very little is known about its biology. While studying nocturnal foraging of *Dinomyrmex gigas* in Singapore, we observed a large and fairly compact group of *Prenolepis subopaca* walking down a tree, before vanishing in leaf litter on the ground.

MATERIALS AND METHODS

In Mandai Forest, Singapore, we collected *Prenolepis subopaca* in two sites located 1 km apart. The first site (1.409°N, 103.784°E) was visited on 5 November 2016, the second site (1.401°N, 103.777°E) on 4 January 2017. Both sites correspond to secondary forest belonging to the ‘abandoned-land forest’ subtype (Yee et al 2016). Such forest patches were regrown from ‘kampungs’ (villages) or plantations abandoned in the 1960s. The sites had a mix of fruiting trees such as *Durio zibethinus* (durian) and plantation trees like *Hevea brasiliensis* (rubber).

Stacked photographs were taken. Voucher specimens are deposited in the Lee Kong Chian Natural History Museum in Singapore.



Fig. 1. Party of about 200 *Prenolepis subopaca* workers walking down a trunk at dusk

Only one species of *Prenolepis* is known from Singapore. *P. subopaca* Emery, 1900 was collected in Sembawang and Bukit Timah (Williams & LaPolla 2016). There is also an unconfirmed record of *P. jerdoni* ('ayer terjun', meaning waterfall in Malay; Overbeck 1924).

RESULTS

Just after dusk (about 18:30 h) in site 1, a large party of *Prenolepis subopaca* workers moved down a tree at least 10m high (Fig. 1). No brood was carried. Ants walked 3-5 abreast following



Fig. 2. Worker of *Prenolepis subopaca* collected from the dusk party, showing marked physogastry, i.e. intersegmental membranes are visible in the gaster.

a distinct trajectory on the trunk. They crossed over to a small horizontal branch, where the trail narrowed down to one or two ants (Electronic Supplementary Material Video S1). Ants continued to a vertical vine connecting the ground and disappeared in the thick leaf litter. We estimate the distance from first to last sightings to be 4–5 m. *Dinomyrmex gigas* foragers were simultaneously active on this very tree.

Examination of photos and video of the trail allowed a guesstimate of 200 individuals (Electronic Supplementary Material Video S2). We checked that brood was not involved, thus excluding a nest relocation. A large proportion of foragers had greatly distended gasters, as seen

in photos and preserved specimens (Fig. 2). We dissected two workers to check that their swollen gaster was not due to ovarian activity.

On another day (site 2), we chanced upon a colony of *P. subopaca* nesting under layers of leaf litter, about 5 to 10 cm deep. An estimated 300 workers (Fig. 3) were present with numerous brood, one winged queen and one male. After disturbance, the ants scattered and ran deeper into the leaf litter carrying their brood (pupae, larvae and eggs). After some time, clear trails were formed and ants travelled along these. A worker carried an isopod along the trail. Ants in this colony lacked enlarged gasters.



Fig. 3. Worker of *Prenolepis subopaca* collected from the nest in leaf litter (site 2)

DISCUSSION

We interpret our sighting (site 1) as a party of successful foragers retrieving honeydew to their nest, as revealed by the swollen gasters. Finding a *P. subopaca* nest in leaf litter some weeks later (site 2) supports that the party observed at dusk was returning home. We assume a substantial honeydew source in the canopy. What benefits may be derived from such synchronized retrieval of honeydew? In most ant species that gather honeydew, foragers walk singly to-and-fro between nest and honeydew source. Since honeydew is collected in the crop ('social stomach'), a forager returns home once there is no room for more fluid. *P. subopaca* presumably move in a group for protection against predators (spiders?) or competing ants.

The timing of our single observation suggests that *P. subopaca* was moving out of the tree before nocturnal ant species become active. Temporal niche separation is especially pronounced in the tropics where uniform temperatures allow 24h activity.

Houadria et al. (2015) used bait and pitfall data to show day and night specialization in a ground ant community. Investigating vertical distribution patterns of ants, Hashimoto et al. (2010) showed that ground-nesting and arboreal-nesting species extended their foraging activity across strata along the tree-trunk. Honeydew is a resource mostly exploited by arboreal ants, but it is not surprising that ground-nesting species also feed on it. Even *Aenictus hodgsoni* (army ants) occasionally collect honeydew on trees, although single foragers went back and forth from a hole in the soil 2m away (Staab 2014).

Cooperative transport is important for the ecology of many ant species (McCreery & Breed 2014). Quick transport of a large food item back to the nest reduces the amount of time the food is vulnerable to competition. Group retrieval is usually associated with live arthropod prey (e.g. Peeters and De Greef 2015), and we are not aware of any examples involving honeydew. In *Formica schaufussii*, the size of foraging groups appeared more important for the defence of arthropod prey than for increasing speed of transport, but retrieval of honeydew was not investigated (Traniello & Beshers 1991). *Prenol-*

epis imparis can recruit up to 200 workers at tuna and syrup baits, and they are highly aggressive at defending these against competing ants (Lynch et al. 1980). Similarly, *P. subopaca* may forage in group to monopolise rich scattered sources of honeydew. We do not know if these are located by scouts that subsequently recruit nestmates, or if large foraging parties roam the canopies.

The ability of adult ants to use the crop as a storage organ contributes greatly to their superior foraging efficiency, as well as an ability to withstand periods of starvation. This novel adaptation is based on a complex proventriculus, a muscular valve that restricts movement of fluids between crop and midgut (Eisner & Wilson 1952). Repletes are especially pronounced in subfamily Formicinae owing to large intersegmental membranes folded between the abdominal sclerites, and which allow substantial expansion of the gaster (Fig. 2). *Prenolepis imparis* workers feeding at a syrup bait gained an average of 130-200% of their original body weight (Lynch et al. 1980). The natural food of *P. imparis* consists of honeydew, nectar from flowers and extrafloral nectaries, juices of dead earthworms or young plant tissues. These various liquids are imbibed in such quantities by the foragers that their gasters become greatly distended and make their gait unsteady (Tschinkel 1987). The occurrence of repletes (also Lőrinczi 2016) appears to be characteristic of *Prenolepis* genus as a whole.

ACKNOWLEDGEMENTS

We thank Jack Longino, Roberto Keller and Yoshiaki Hashimoto for comments, and Weeyawat Jaitrong (Thailand Natural History Museum, Bangkok) for species identification. Wildlife Reserves Singapore Conservation Fund gave financial support and access to Mandai forest.

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APPENDIX

Electronic Supplementary Material Video S1
Synchronized mass return of *Prenolepis* honeydew-gatherers (described in Results).
<Prenolepis night trail Peeters.mp4> (32 seconds) 82MB

Electronic Supplementary Material Video S2
Prenolepis honeydew-gatherers returning to ground nest (concurrent recording as S1).
< Prenolepis night trail Gordon.mov > (42 seconds) 58MB

ASIAN MYRMECOLOGY

A Journal of the International Network for the Study of Asian Ants

Communicating Editor: Adam L Cronin