

## Evidence of predation in two species of the *Colobopsis cylindrica* group (Hymenoptera: Formicidae: Camponotini)

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**ABSTRACT.** The complex ecology and nutrition of “exploding” ants of the *Colobopsis cylindrica* group (COCY) is still poorly understood. Hitherto, this group of ants was thought to feed mainly on phylloplane biofilms with only scarce observations of carnivorous behaviour. This study focusses on observations and behavioural experiments conducted on *Colobopsis badia* and *Colobopsis leonardi*, two species native to Thailand. In experiments with *C. leonardi*, we investigated recognition and acceptance of diverse arthropod prey, as well as its mode of transport into the nest. In addition, preliminary data on *C. badia* were collected. We present the first recorded instances of predation for these species and discuss our findings in the light of previously published hypotheses on COCY nutrition and behaviour.

**Keywords:** carnivory, exploding ants, nutrition, Southeast Asia, Thailand

### INTRODUCTION

The “exploding” ants of the *Colobopsis cylindrica* group (COCY) are particularly known for their self-sacrificing defensive behaviour (autolysis), but have also been the object of several ecological studies (e.g., Cook 2008, Davidson *et al.* 2007, 2009, 2016; Laciny *et al.* 2018). However, the nutrition of imagines and larvae still remains an unanswered question. Isotopic evidence from six examined Bornean COCY spe-

cies points to plant exudates or microbes from the phylloplane biofilm as their primary source of nitrogen (Davidson *et al.* 2016). During extensive observations at the Kuala Belalong Field Studies Centre (KBFSC) in Brunei Darussalam, workers have never been observed to hunt or feed on animal carcasses. However, fragments of unidentified arthropod exoskeletons have been found within the buccal pellets of COCY workers (Davidson *et al.* 2016).

In feeding experiments carried out at the same location between 2015 and 2017, two COCY species, *Colobopsis explodens*, Laciny & Zettel 2018, and an undescribed species related to *Colobopsis leonardi* Emery, 1889, accepted various offered food items (fish, fruit, biscuit crumbs), but only transported small dead insects and arthropod body parts. In experimental settings, no instance of feeding on spores or hyphae of filamentous fungi (such as molds) was observed, but a suspension of yeasts was accepted (M. Rahimi, unpublished data). However, on their foraging grounds, workers were frequently seen plucking mosses, lichens and fungi from the surface of bark or leaves (“grazing”), which has previously been hypothesized to contribute to their nutrition (Laciny *et al.* 2018, compare Davidson *et al.* 2007, 2016).

It is well known that ant larvae require protein-rich nutrition during their development (e.g., Hölldobler & Wilson 1990, Dussutour & Simpson 2009). How these needs are met in larvae of the COCY group is hitherto unknown. However, several reports of arthropod carcasses being accepted and transported into the nest indicate that COCY larvae may be fed with animal protein: Hashimoto *et al.* (1997) reported that “*Camponotus saundersi* Emery, 1889” (species identity unconfirmed) accepted freshly killed mosquitoes in an experimental setting on Borneo, and Yamamoto *et al.* (2009) reported that *Colobopsis* sp. nr. *leonardi* in Indonesia fed on offered mealworms. Another author (W. Jaitrong, unpublished data) has observed that *Colobopsis leonardi*, a common COCY species in Thailand, carries insect prey. Moreover, a mermithid infection of adult ants of *Colobopsis* sp. nrSA in Brunei suggests that earthworms or insects were fed to the ants’ larvae: Mermithid nematodes are known to be transmitted when intermediate hosts (oligochaetes or aquatic insects) containing the nematodes’ infective larval stages are fed to the host ants’ larvae (Kaiser 1986, Poinar 2012, Laciny *et al.* 2017). These findings suggest that contrary to previous hypotheses, these ants’ nutrition is not solely based on plants and microorganisms of the phylloplane biofilm but also includes some form of animal predation.

When animal prey is carried into the nest, ants are known to employ different tech-

niques of transport: Yamamoto *et al.* (2009) compared different modes of prey transport between arboreal and ground-nesting ants of Southeast Asia. Among the studied species was “*Colobopsis* sp. nr. *leonardi*” – presumably a member of the COCY group. The study found that this species, as well as the vast majority of other arboreal species, divided large prey into smaller pieces that were then carried into the nest by individual workers without cooperation. In contrast, ground-nesting ants tended towards cooperative retrieval of prey. Furthermore, the mode of prey transport by individual ants is influenced by the size and weight of the transported item: Small items are preferentially lifted while the ant is facing forward; heavy or large items are dragged while the ant walks backwards (Sudd 1960; see Czaczkes & Ratnieks 2013 for a review). We aimed to assess whether these correlations are also applicable to the examined COCY species.

Finally, we attempted to investigate the use of different nest entrances for bringing prey into the nest. COCY ants are polydomous with large colonies containing many thousands of individuals (Federle *et al.* 1998, Laciny *et al.* 2017, Laciny *et al.* 2018). Especially members of the *C. saundersi* complex willingly and rapidly colonize artificial nests and use them to rear their brood (Davidson *et al.* 2009, Laciny *et al.* 2017, Laciny *et al.* 2018). This suggests a form of nest partitioning also corroborated by the presence of carton partitions in detached nest fragments (A. Kopchinskiy, I. Druzhinina, unpublished data). This may result in the allocation of protein-rich animal prey to specific parts of the nest.

Molecular and morphological analyses (Cook 2008, Laciny *et al.* 2018, Zettel *et al.* unpublished data) have identified at least three distinct subclades native to Southeast Asia: The *C. saundersi* complex, the *C. leonardi* complex, and the eponymous *C. cylindrica* complex. In this paper, we describe observations and standardized experiments on selected colonies of two COCY species, *Colobopsis leonardi* from the *C. leonardi* complex and *Colobopsis badia* from the *C. saundersi* complex, in the Khao Chong Botanical Garden in southern Thailand.

We aimed to assess prey recognition and acceptance by offering various living and dead arthropods and oligochaetes. In addition, we re-

corded the modes of transport employed by ants dealing with prey items of different species and sizes, as well as differential utilization of available nest entrances. We present the first evidence of insect predation and acceptance of animal prey for the studied species and interpret our results within the framework of previous studies on the enigmatic nutrition of the COCY group.

## MATERIAL AND METHODS

### 1. Specimens, depositories and identification

Studies were carried out on June 6–7, 2016 in the Khao Chong Botanical Garden, Trang Province, southern Thailand. Both colonies were found at the sides of a trail leading from a parking area to the Ton Pliw Waterfall (N 07°32'34" E 99°47'33", ca. 150 m a.s.l.).

*Colobopsis leonardi* and *Colobopsis badia* were identified by comparison with the types deposited in the Museo Civico di Storia Naturale Giacomo Doria (Genova, Italy) and the Oxford University Museum of Natural History (United Kingdom). The herein examined specimens of *C. badia* were analysed via DNA barcoding at TU Vienna (Laciny *et al.* 2018) to confirm species identity. Specimens of the ant *Acropyga acutiventris* Roger, 1862 were identified using the key of LaPolla (2004). Termite specimens were identified by S. Syaukani using the keys by Ahmad (1958), Thapa (1981), and Tho & Kirton (1992). Reference specimens of all taxa will be deposited in the Thailand Natural History Museum and in the Natural History Museum Vienna, of termite species also in the Syiah Kuala University, Banda Aceh.

### 2. Observations on *C. leonardi*

#### 2.1. Observed colony and experimental setup

The studied colony of *C. leonardi* (colony no. 66-8) inhabited a fallen branch of a rambutan tree (*Nephelium lappaceum* L., Sapindaceae). It is unknown whether more nest sites of the colony existed in the canopy of the neighbouring trees. The branch (Figure 1) had a total length of more than five metres and a width of about 20 cm, the distance between the entrances E and W was about 3.7 m, between E and N about 0.4 m (en-

trances termed according to approximate cardinal direction). Entrance W consisted of a single hole, entrances E and N of two holes in close vicinity (ca. 3 and 7 cm apart, respectively); the round entrance holes had a diameter of ca 3–5 mm. A trail between entrances E and W was used by foraging workers continuously and in high frequency in both directions, constituting the majority of the observed worker activity.

#### 2.2. Prey recognition and entrance selection

First, various arthropods, arthropod body parts, and earthworms were offered at the trail of *C. leonardi* (Table 1). During these experiments, it was observed that the entrance the prey was transported to was strongly biased towards entrance E. For the following experiments concerning the selection of entrances, the branch section between entrances E and W was divided into five sections of ca. 75 cm length (1–5, numbering starting at entrance E). Single prey items were offered by alternating between sections, starting at one and ending at five. Four species of prey (*Coptotermes curvignathus* Holmgren, 1913 (Rhinotermitidae, Coptotermitinae); *Macrotermes gilvus* (Hagen, 1858) (Termitidae, Macrotermitinae); *Nasutitermes havilandi* (Desneux, 1904) (Termitidae, Nasutitermitinae); *Acropyga acutiventris* Roger, 1862 (Formicidae, Formicinae)) were used for these experiments. Standardized experiments took place on two consecutive days: *C. curvignathus* termites and *A. acutiventris* ants were used as prey items on the first day, *M. gilvus* termites on the second day. Because insect specimens quickly moved away from the ant trail and fell off the branch, prey animals were killed by crushing their head just before offering and placed in the approximate middle of the respective section on the ants' trail. *N. havilandi* termites were only used during preliminary observations. Only in one experimental setting, living *Macrotermes gilvus* termites were offered.

Number of encounters of prey by COCY ants until transport was noted; "1" means that the first ant that encountered the prey took it up and carried it to a nest entrance (Figure 4). In addition, it was recorded whether prey items were transported by single workers or cooperatively. After it was observed that some prey-carrying ants enter the nest entrance reversed, with gaster first,

**Table 1.** Prey specimens / body parts offered to *Colobopsis leonardi* during feeding experiments, including number of observations and behaviour of foraging workers. Species denoted with an asterisk (\*) were used for standardized experiments.

Order	Specified	Part offered	#Obs.	Behaviour / mode of transport
Isoptera	* <i>Macrotermes gilvus</i>	entire	20	carried to nest in one piece
Isoptera	* <i>Coptotermes curvignathus</i>	entire	10	carried to nest in one piece
Isoptera	<i>Nasutitermes havilandi</i>	entire	8	carried to nest in one piece
Thysanoptera	unidentified (ca. 4 mm)	entire	1	carried to nest in one piece
Hymenoptera	<i>Odontomachus rixosus</i>	entire	1	carried to nest in one piece, cut apart before entering
Hymenoptera	<i>Anoplolepis longipes</i>	entire	1	carried to nest in one piece
Hymenoptera	* <i>Acropyga acutiventris</i>	entire	15	carried to nest in one piece
Coleoptera	Melolonthidae	leg	1	carried to nest in one piece
Coleoptera	Melolonthidae	abdomen	1	carried to nest in parts, liquids probably consumed
Coleoptera	Tenebrionidae (ca. 8 mm)	entire	1	carried to nest in parts
Coleoptera	pupa (ca. 10 mm)	entire	1	integument opened to consume liquids, carcass transported
Isopoda	unidentified (ca. 7 mm)	entire	1	carried to nest in one piece

the orientation upon entering was studied during most of the experiments (38 out of 45) (Figure 5). A few living specimens of *Macrotermes gilvus* were placed on the ant trail in zone one to observe how *C. leonardi* reacts in contact with more aggressive insects. During encounters, the tip of a pencil was used to change direction of termites to keep them on the trail.

### 3. Observations on *C. badia*

Workers of a *C. badia* colony (colony no. 66-4) were observed on leaves of low vegetation and on lianas leading up to two small trees (breast height diameter ca. 20 cm) (Figure 2). Nest entrances were not found; they were most probably located higher up in the tree, as is often the case in COCY colonies (Laciny *et al.* 2018). Feeding experiments were carried out on June 6, at around 10:30 a.m. when a moderately high activity of workers (higher than on the previous and following days) was observed on an ant trail on a ca. 2 cm thick liana ca. 0.5 m above ground. As a preliminary feeding experiment, three freshly killed speci-

mens of *C. curvignathus* termites were placed on the liana at a distance of ca. 5 cm from each other and the ants' behaviour was recorded.

### 4. Morphometry and statistical analysis

To assess body size of ants and their prey (Table 2), random samples of the studied *C. leonardi* and *C. badia* colonies (n = 10 for each species), as well as three species of termites and specimens of the ant species *Acropyga acutiventris* (*C. curvignathus*, n = 12; *M. gilvus*, n = 11; *N. havilandi*, n = 8; *A. acutiventris*, n = 10) were taken at the study site and stored in 96% ethanol. Measurements were conducted at NHM Vienna with a Nikon SMZ1500 binocular microscope. Termites were measured in wet condition; ants were dry-mounted on triangular glue-boards prior to measuring.

#### Measurements taken:

HW Head width. Maximum width of head in full-face view.

**Table 2.** Minimum and maximum values (mm) of head width (HW) and total body length (TL) for *Colobopsis leonardi* (n = 10), *Colobopsis badia* (n = 10), *Acropyga acutiventris* (n = 10), and three species of termites – *Coptotermes curvignathus* (n = 12), *Macrotermes gilvus* (n = 11), and *Nasutitermes havilandi* (n = 8). \*maximum values of *Macrotermes gilvus* are of soldiers.

	<i>C. leonardi</i>	<i>C. badia</i>	<i>N. havilandi</i>	<i>C. curvignathus</i>	<i>M. gilvus</i>	<i>A. acutiventris</i>
HW <sub>min-max</sub>	1.55 - 2.35	1.46 - 1.59	1.13 - 1.25	1.31 - 1.50	1.63 - 3.00*	0.81 - 0.94
TL <sub>min-max</sub>	6.52 - 10.96	5.64 - 6.23	2.88 - 3.56	3.38 - 5.00	3.81 - 8.50*	2.69 - 3.44

TL Total body length. For termites: from tip of mandibles to tip of abdomen; for ants: added lengths of head (excluding mandibles), mesosoma, petiole, and gaster.

These measurements were then used to compare the size ranges of the offered prey species and assess whether prey items of different sizes were treated differently regarding the ants' acceptance and mode of transport.

To compare numbers of encounters until acceptance by an ant, the mean number of encounters was calculated for each prey species (Figure 4). Limits for 95% confidence intervals were obtained via Bootstrap (10,000 resamplings). All analyses were performed in Past3 (Hammer *et al.* 2001) and graphed in MS Excel 2010.

## RESULTS

### 1. First observations on *Colobopsis leonardi* and variety of food taken

In the morning of June 6, high activity was observed on an ant trail on the upper side of a fallen branch of a rambutan tree colonized by *C. leonardi*. To test predatory behaviour, worker specimens of *C. curvignathus* termites were collected under a distant piece of wood and offered alive. Each termite was killed by the bites of a single *C. leonardi* worker and carried away. During these observations a trail of *Nasutitermes havilandi* was noticed on the underside of the branch. Workers and soldiers of this rather small termite species were also offered at the ants' trail, and were also carried away by the ants. It was observed that all termites were carried towards the eastern end of the branch.

### 2. Arthropod and oligochaete prey taken by *Colobopsis leonardi*

Insects and woodlice, all from the surrounding of the nest site or from the botanical garden's headquarters were offered at the ants' trail (listed in Table 1; Figure 3). All items were carried to the nest, some were cut into fragments before transport or only their liquid or soft inner parts were consumed or carried, respectively. Pieces of earthworms were accepted as well.

### 3. Standardized experiments with *Colobopsis leonardi* on prey acceptance and entrance selection

In many cases (19 of 45; 42%), the first ant that encountered the insect prey took it up and carried it away. In the other 26 experiments, 2–10 contacts were counted, amounting to a total average of 2.5 encounters. The insects were always carried into the nest within ca. 5 minutes (maximum) after placement. There was a clear difference between the prey species: The number of encounters until an item was carried off was considerably lower in *Coptotermes curvignathus* (on average 1.7 encounters) compared to *Macrotermes gilvus* (on average 3.2 encounters), but did not differ to such a noteworthy extent between *Acropyga acutiventris* (3.07 encounters on average) and the other two prey-groups (Figure 4). In most instances of encountering but rejecting prey (n = 64), it was not clear whether the ant just stumbled upon the item or recognized and neglected it, but in three other instances (all with *M. gilvus*-workers) the behaviour was more obvious: Once an ant examined the termite and clearly neglected it. In a second instance, an ant

examined the prey but was disturbed by another ant. In a third instance, a very small ant examined and lifted the termite, but was too weak to carry it. For size comparisons of *C. leonardi* with the respective prey species see Table 2.

Prey carrying to different nest entrances was strongly biased. In the standardized experiment with termites and ants, 43 out of 45 items (95.5 %) were carried to entrance Ea, one each to Eb and Na, and none to Nb and W, independent of the distance to the site where the prey was offered. It is interesting to note that the two deviating observations (entrances Eb and Na) both happened with *C. curvignathus* as prey and one after another, suggesting that there was a “reason” why entrance Ea was not used for a short while. During further observations, one item was carried into entrance W: a small thrips that was already found near entrance W and then placed directly on the ant trail a few centimetres from the entrance.

#### 4. Experiments with *Colobopsis leonardi* and living *Macrotermes gilvus* termites

Experiments with offering living termites proved difficult, because the termites often escaped from

the ant trail before they were detected by the ant workers. In addition, the pencil used to keep termites on the trail frequently disturbed the ants and made observations time-consuming. Therefore, only a few observations were done with *M. gilvus* termites:

In three instances ant workers killed termite workers by biting and carried them into the nest entrance Ea. On one occasion a small *M. gilvus* soldier was bitten by ant workers twice, but the termite shooed the ants away; however, it died from the bites and was carried to entrance Ea when it was dead. Large *M. gilvus* soldiers (Table 2) were usually avoided by the ants except for one instance: An ant worker attacked the termite from its back and bit it. The soldier turned around, snapped with its powerful mandibles and decapitated the ant. No instances of suicidal defensive behaviour (autothysis) were recorded during the experiments.

#### 5. Carrying food along trail and into the nest

All small prey items were taken up with the mandibles, lifted and brought to the nest entrance by single workers. Cooperation for dragging larger



**Fig. 1.** Branch on forest floor, where experiments with *Colobopsis leonardi* were carried out: 1–5: sections of experiments. Ea, Eb, Na, Nb, W: nest entrances (Na and Nb are on a side branch facing the viewer). Insert shows close-up view of entrances Ea and Eb. © H. Zettel



**Fig. 2.** Foraging area of *Colobopsis badia*, where observations were made. Arrows mark the tree stems and the liana with ant trails. © H. Zettel

items was never observed. In contrast, the transport of medium-sized items, which could be dragged but not lifted by a single worker was slowed down or made almost impossible by further workers. In one instance, a single worker tried to drag the remains of a beetle pupa to the nest, but was hindered to do so for more than 20 minutes by other workers who tried to do the same. Only when the activity on the trail became low, the worker brought the item into the nest.

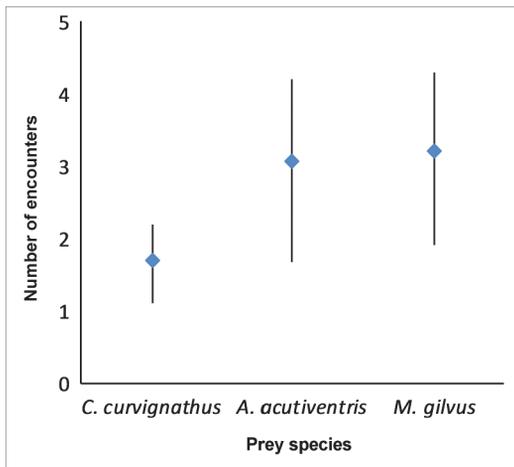
While ants without prey always entered the nest with the head first ( $n = 100$ ), prey-carrying ants often changed their behaviour and entered the nest with the gaster first (73.7%). There were differences between prey species: *Coptotermes curvignathus* prey was carried exclusively gaster first, whereas both orientations were observed when carrying *Acropyga acutiventris* (53.3% gaster first) and *Macrotermes gilvus* (70% gaster first) (Figure 5).

## 6. Preliminary observations on *Colobopsis badia*

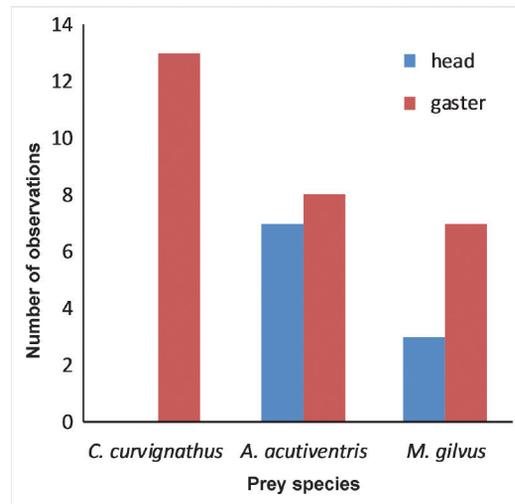
Three specimens of *C. curvignathus* termites were offered on the ants' trail. Ant workers approaching this area shrunk back without touching the *C. curvignathus* specimens and/or alarmed nest mates with highly raised gasters. The area was subsequently avoided by most (not all) workers which then used a liana running parallel to the first one. During the time of observation, a *C. badia* worker was observed carrying a small item. Worker and item were caught and preserved. The item was a very small male ant (presumably Dolichoderinae). About 20 minutes after the placement of *C. curvignathus* on the trail a *C. badia* worker examined one of them, took up a piece and carried it away. It was observed carrying it for about one meter along the liana trail before it was lost from sight. After further 20 minutes without relevant observations, the experiment was stopped.



**Fig. 3.** Minor workers of *Colobopsis leonardi* take various prey: (A) scarabaeid beetle thorax and abdomen; (B) scarabaeid beetle abdomen; (C) fragments of *Odontomachus rixosus* ant; (D) beetle pupa. © W. Jaitrong



**Fig. 4.** Number of encounters by workers of *Colobopsis leonardi* until transport of a prey item for three different prey species; blue diamonds denote mean number of encounters, black lines represent 95% confidence intervals of means.



**Fig. 5.** Observations of *Colobopsis leonardi* workers carrying prey items of three different species into the nest, either head first (blue) or gaster first (red). Number of observations per species: *C. curvignathus* n=13, *A. acutiventris* n=15, *M. gilvus* n=10.

## DISCUSSION

### 1. Carnivory

Some species of COCY ants, including *Colobopsis leonardi*, are dominant species of tropical Southeast Asia and often occur in huge colonies (Laciny *et al.* 2017). However, there are hardly any observations and only two publications (Hashimoto *et al.* 1997, Yamamoto *et al.* 2009) on COCY ants carrying or taking animal prey. Also, during fieldwork in Trang Province, Thailand, during several days of observations of *C. leonardi* trails, the first author was not able to spot a single worker transporting a solid item except for the experimental settings. Such a lack of observations has led to alternative hypotheses about COCY nutrition (e.g., Davidson *et al.* 2016). The experiment described here provides evidence that *Colobopsis leonardi* accepts a considerable variety of arthropods (and even pieces of earthworms) when offered, possibly for feeding the larvae. It will need further experiments and observations to prove whether other COCY species behave in the same way. Preliminary observations on *Colobopsis badia* indicate differences in acceptance of larger prey items.

The fact that the experiments on *C. leonardi* were conducted on a (likely) fragmented colony located in a fallen branch, must be considered when interpreting the results, as this may have put condition-specific stress on the ants. During an observation in the following year, the nest fragment was abandoned. However, previous observations of several COCY species (Laciny *et al.* 2017, 2018) have demonstrated that these ants will easily colonize new nesting sites and even maintain contact between artificial nests, broken branches, and the main part of the nest. In addition, the new observations presented herein are corroborated by feeding experiments conducted in the two previously published studies (Hashimoto *et al.* 1997, Yamamoto *et al.* 2009) as well as preliminary observations by the authors in Brunei (Laciny *et al.* 2018). Most likely, COCY ants utilize a wider variety of resources than previously hypothesized, also including animal prey.

### 2. Prey recognition and transport

In feeding experiments with *Colobopsis leonardi*, those prey items that were eventually taken into the nest were recognized and transported by foraging workers within a few minutes. Especially *Coptotermes curvignathus* termites were often accepted by the first worker to encounter them. Although the other two prey species took significantly more encounters (ca. 3 workers on average), they too were accepted and transported within the first five minutes after offering. We observed no decline of prey acceptance during the course of the experiment or on the second day of testing, which would indicate satiation or decreasing necessity for food within the colony.

During the experiments conducted for this study, no instance of cooperation for prey transport was ever observed in COCY ants. This finding agrees with the previously published records of lacking cooperation in arboreal species in contrast to cooperative prey retrieval in ground-nesting ants (Yamamoto *et al.* 2009). The reason for this difference in prey transport is still unclear. One possible explanation (put forth by Davidson *et al.* 1998) is that fragmentation before transport is more time consuming and has a higher risk of interference by other predators, and is therefore preferentially utilized by dominant or aggressive species, which would be the case in COCY ants. In addition, cooperatively transporting large prey items may simply be impractical for arboreal species, especially when moving along thin branches (Czaczkes & Ratnieks 2013).

The expected correlation between prey size and either forward- or backward facing mode of transport (Sudd 1960, Czaczkes & Ratnieks 2013) did not hold true for the observed colony of *Colobopsis leonardi*: While all items were first picked up and carried forward along the trail, at the nest entrance, one variety of prey (*Coptotermes curvignathus* termites) was exclusively transported walking backwards, while the other species (*Macrotermes gilvus* termites and *Acropyga acutiventris* ants) were brought in by both backward- and forward-facing workers. The different mode of transport was likely not caused by the different size or weight of the prey species, as *C. curvignathus* was not the largest prey item offered and the change in direction occurred only

directly before entering the nest. In the previously investigated species *Colobopsis explodens* (Laciny et al. 2018) a peculiar guarding behaviour was observed: A small number of workers always stayed close to the entrance and seemingly monitored the entering and leaving of foragers. It is possible that an ant carrying a potential enemy as prey would be barred from entering the nest by guards within and must therefore present its gaster to be recognized as a colony member. Why this was not observed with all prey species, however, is unclear. It may also be the case that other factors – such as the size and shape of the nest entrance – influenced this behaviour. The exact reasons for this phenomenon should be investigated in the course of further studies.

Another interesting finding of the present study was the obviously biased use of one particular nest entrance when *C. leonardi* workers were carrying prey items. Many ants are known to exhibit spatial fidelity when foraging (e.g., Mersch et al. 2013), which may lead to the assumption that the preferential use of one nest entrance was linked to entrance fidelity of the observed workers. However, the main activity of workers was observed between nest entrances located at opposite ends of the branch, indicating that there may not have been a connection between the entrances inside the nest. The placement of food items on different branch sections also had no observable effect on entrance selection, so that mere distance to the entrance can be excluded as a reason. Based on previous observations (e.g., Laciny et al. 2017, 2018), the investigated species is likely polydomous and may utilize specific partitions on the nest for specialized purposes, such as rearing brood. We therefore deem it likely that the entrance selection observed in the present study was due to the internal architecture of the *C. leonardi* nest, possibly because the protein-rich arthropods and oligochaetes were transported directly to the ants' brood located in a specific chamber.

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