SOME NOTES ON THE TOOL-USING BEHAVIOUR OF THE ANT, *APHAENOGASTER SUBTERRANEA* (HYMENOPTERA: FORMICIDAE)

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Abstract. Ants of the genus *Aphaenogaster* lack the ability to ingest and carry large volumes of liquid food and share it through trophallaxis with other colony members in the nest. Nevertheless, these species have developed a complex method to compensate for these deficiencies by using small objects as tools to transport liquid food back to the colony. In the present study, I investigated the tool-using behaviour of *Aphaenogaster subterranea* in retrieving food through field observations using honey and petroleum jelly baits. Similarly to other members of its genus, the tool-using behaviour of the foraging workers of *A. subterranea* consisted of three distinct components at honey baits, dropping tools into the liquid food, adjusting the position of tools brought by other workers, and transporting the food-soaked tools back to the colony. The proportion of tool-using workers constituted only a small fraction of the total number of workers that were observed at baits, however, the number of workers manipulating tool items was positively correlated with the number of workers performing other activities. Materials most commonly used as tools were particles of soil and easily moveable, broken fragments of plant materials (e.g., bits of pine needle, cone and bark). Tool-using workers also dropped some debris into petroleum jelly, a non-food substance presenting a potential hazard of drowning or becoming entangled, at 60% of the baits, however, at a significantly lower intensity than in the case of honey. Adjusting or removing tool items soaked with petroleum jelly, on the other hand, was never observed.

Key words: Aphaenogaster subterranea, food transport, foraging, tool use.

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Introduction

Tool use, according to St. Amant and Horton's (2008) definition, is "...the exertion of control over a freely manipulable external object (the tool) with the goal of (1) altering the physical properties of another object, substance, surface or medium (the target, which may be the tool user or another organism) via a dynamic mechanical interaction, or (2) mediating the flow of information between the tool user and the environment or other organisms in the environment". Although the most diverse forms of tool-using behaviour are a characteristic of passerine birds and primates, the occurrence of tool use is fairly widespread in animals, and it has been described in members of eight classes in three phyla (Mollusca: Gastropoda, Cephalopoda, Arthropoda: Malacostraca, Arachnida, Insecta, Chordata: Actinopterygii, Aves, Mammalia) (Bentley-Condit and Smith 2009).

In ants, one of the most well-known forms of tool use occurs among weaver ants of the genera *Oecophylla*, *Polyrhachis* and *Camponotus*. These ants build their nests made of leaves stitched together using the silk produced by their larvae, which are held and manipulated by workers during nest construction (Hölldobler and Wilson 1990). Other species, such as *Dorymyrmex bicolor* or *Aphaenogaster cockerelli* use small stones and other objects to plug the nest entrances of their competitors (Möglich and Alpert 1979, Barton *et al*. 2002.). Lin (1964-65) described a similar behaviour in *Tetramorium caespitum* (recently *Tetramorium* sp. E, cf. Steiner *et* *al*. 2008), whose workers used sand grains while attacking a halictine bee, *Lasioglossum zephyrum*.

The third form of tool use exhibited by ants is when foraging workers drop debris (e.g., particles of soil, bits of leaf, etc.) into liquid food, and then transport the food-soaked tools back to the colony. This type of behaviour is a characteristic of *Aphaenogaster* species, and has been described for eight species of this genus (Fellers and Fellers 1976, Tanaka and Ono 1978, Fowler 1982, McDonald 1984, Agbogba 1985, Cerdá *et al*. 1988, Banschbach *et al*. 2006), but it also occurs in *Pogonomyrmex badius* (Morrill 1972) and *Solenopsis invicta* (Barber *et al*. 1989). In *Aphaenogaster* species, liquid food is utilized more efficiently by tool use than by internal transport; furthermore, this behaviour may increase the ability of these species to compete more successfully with other ant species (Fellers and Fellers 1976, Tanaka and Ono 1978).

In this study, I investigated the tool-using behaviour of *Aphaenogaster subterranea* in retrieving food through field observations, and attempted to answer the following questions: (1) What types of behaviour patterns do tool-using workers exhibit? (2) What is the ratio of workers that perform these tasks? (3) What types of tools are used? (4) Are there any differences in reaction of tool-using workers to liquid food and to non-food viscous liquids that present a potential hazard of drowning or becoming entangled?

Materials and methods

Study species

Aphaenogaster subterranea (Latreille, 1798) is a widely distributed Mediterranean myrmicine ant, which occurs in Central and Southern Europe, Moldova, Southern Ukraine, Crimea, Asia Minor and the Caucasus (Kutter 1977, Czechowski *et al*. 2012). It is a highly thermophilous species, inhabiting mostly moderately wet and warm deciduous forests and forest edges (Kutter 1977, Seifert 2007, Czechowski *et al*. 2012), but also occurs in pine forests (Garrido *et al*. 2002, Lőrinczi 2008, 2011, Castracani *et al*. 2010) and occasionally in dry grasslands (Csősz *et al*. 2002, Dekoninck *et al*. 2007, Seifert 2007). It nests under stones, in the soil, leaf litter and occasionally inside and/or under fallen branches (Seifert 2007, Lőrinczi 2011, Stukalyuk and Radchenko 2011, Czechowski *et al*. 2012). Colonies are monogynous and range in size from several hundred to several thousand workers (Schmid-Hempel and Crozier 1999, Seifert 2007, Stukalyuk and Radchenko 2011, Czechowski *et al*. 2012). It is an omnivorous ant, and like other species in the genus *Aphaenogaster*, also uses tools (e.g., particles of soil, bits of leaf, etc.) to transfer liquid food back to the colony (Agbogba 1985, Lőrinczi pers. obs.). Nuptial flights are from the end of July to the beginning of September (Seifert 2007). Although *Aphaenogaster* species are generally classified as opportunists using Andersen’s (1995, 1997, 2010) functional group scheme (e.g., Wike *et al*. 2010), *A subterranea*, contrary to Castracani *et al*.’s (2010) classification, is categorized as cryptic by Gómez *et al*. (2003).

Study area

Field work was carried out in the pine forest on the south-facing slope of Mogyorós-hegy (Mogyorós Hill), located in the middle of the Balaton Uplands in mid-western Hungary (latitude N 47° 05' 47.22", longitude E 18° 01' 29.52", altitude 220 m, dip angle 5-10º). The climate in this region is mild, with a mean annual temperature of 10-15 ºC and mean annual precipitation of 650-700 mm (Füleky *et al*. 2007). The vegetation in the study area is predominantly composed of planted black pine (*Pinus nigra*) stands mixed with young deciduous trees, mostly manna ash (*Fraxinus ornus*).

Field work

The tool-using behaviour of *A. subterranea* in retrieving food was assessed using bait experiments on four days in August 2013. For baiting, four sets of baits, separated by ca. 15 m were randomly located. Each set consisted of five baits placed on the ground along a line transect at 3-m intervals. Baits were plastic discs (8 cm in diameter) (see Fig. 5) with a quarter-teaspoon of honey and petroleum jelly as bait substances placed ca. 5 cm apart from each other. Petroleum jelly was used to test the hypothesis whether debris dropping also functions to protect workers from drowning or becoming entangled in non-food viscous liquids.

On each day of the experiment, the number, localization and behaviour of foraging workers at baits were recorded every 20 minutes for four consecutive hours from 6:20 am to 10:20 am. During each 1-minute observation period, the following behaviour patterns were distinguished: (1) feeding on bait substances ("feeding"); (2) being present at baits without any significant activity ("present"); (3) dropping tools into bait substances ("dropping"); (4) adjusting the position of tools ("adjusting"); (5) transporting food-soaked tools from the bait back to the colony ("transporting").

Results

During the experiment, the most abundant and frequent ant species recorded in the study area was *A. subterranea*, other ants (e.g., *Temnothorax* spp., *Formica* spp., *Camponotus* spp.) occurred only sporadically at baits.

Overall, significantly more workers of *A. subterranea* were recruited to honey baits than to petroleum jelly baits (Wilcoxon signed rank test, z=9.55, p<0.001, n=123) (Fig. 1).

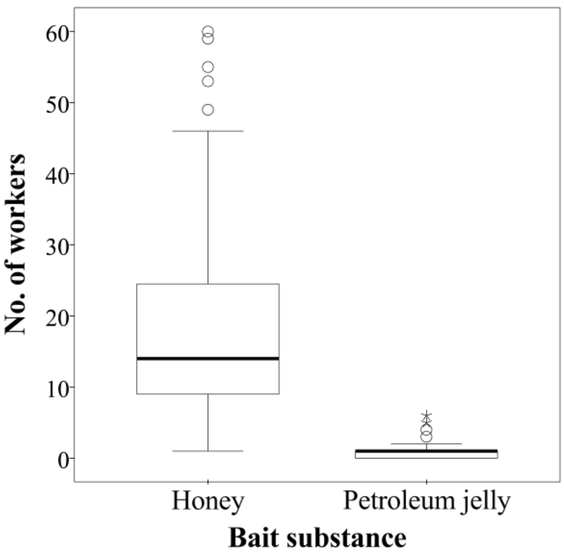

Fig. 1. Bait substance preference of the foraging workers of *Aphaenogaster subterranea*. Boxes indicate the interquartile range; horizontal lines in the boxes indicate the medians; whiskers include all points to 1.5 times the interquartile range; open circles indicate outliers; asterisks indicate extreme outliers.

The tool-using behaviour of foraging workers visiting honey baits consisted of three distinct components that were usually performed by different individuals: (1) selecting, picking up, carrying and dropping tools into the liquid food until its surface was entirely covered; (2) adjusting the position of tools brought by other workers in order to be soaked fully with food; (3) removing and transporting food-soaked tools from the bait back to the colony. In one case, however, it was observed that a worker did not drop the carried tool item into the food, but started to dip it, and then immediately transported it away.

Although the number of workers manipulating tool items was significantly lower than the number of workers performing other activities (Wilcoxon signed rank test, z=9.41, p<0.001, n=123) (Fig. 2), there was a positive correlation between them (Spearman's correlation test, r=0.54, p<0.001, n=123), i.e., the more workers visited the baits, the more exhibited some form of tool-using behaviour.

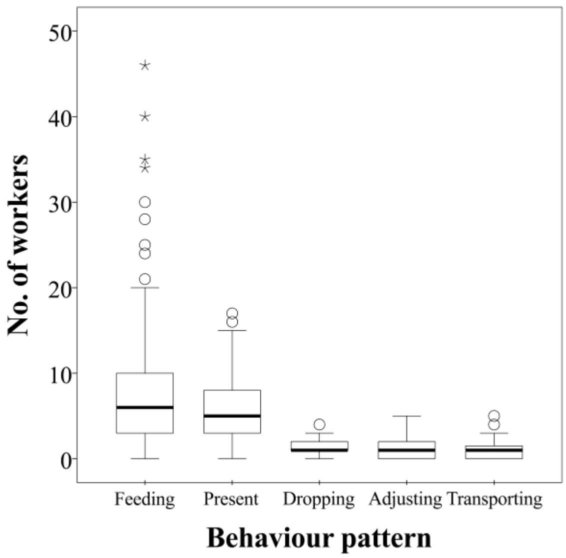

Fig. 2. Behaviour patterns exhibited by the foraging workers of *Aphaenogaster subterranea* at honey baits. Boxes indicate the interquartile range; horizontal lines in the boxes indicate the medians; whiskers include all points to 1.5 times the interquartile range; open circles indicate outliers; asterisks indicate extreme outliers. /"feeding"/: feeding on honey; /"present"/: being present at baits without any significant activity; /"dropping"/: dropping tools into honey; /"adjusting"/: adjusting the position of tools; (5) /"transporting"/: transporting food-soaked tools back to the colony.

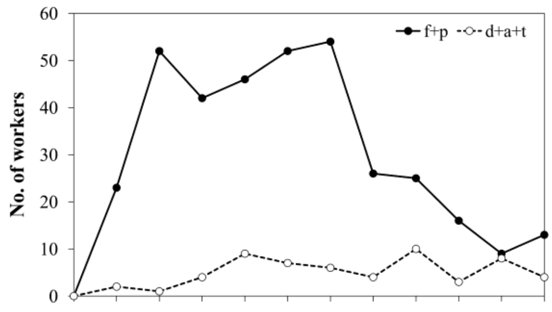

Fig. 3. Temporal dynamics of the number of foraging workers exhibiting different behaviour patterns at a honey bait in the case of one of the studied colonies of *Aphaenogaster subterranea*. /f+p/: feeding workers and workers being present at the bait without any significant activity ("feeding" + "present"); /d+a+t/: tool-using workers ("dropping" + "adjusting" + "transporting").

In the case of the more active colonies of *A. subterranea*, which recruited a larger number

(>40) of workers to baits, the number of workers manipulating tool items remained relatively constant during the survey period, while the number of workers performing other activities decreased shortly after an initial increasing and saturation (Fig. 3).

Although petroleum jelly was usually ignored by visiting workers, it provoked a fleeing or offensive reaction from some individuals after a short antennation. In addition, workers dropped some debris into petroleum jelly at 60% of the baits, however, at a significantly lower intensity than in the case of honey (Wilcoxon signed rank test, $z=8.41$, $P<0.001$, $n=123$) (Fig. 4). Adjusting or removing tool items soaked with petroleum jelly, on the other hand, was never observed.

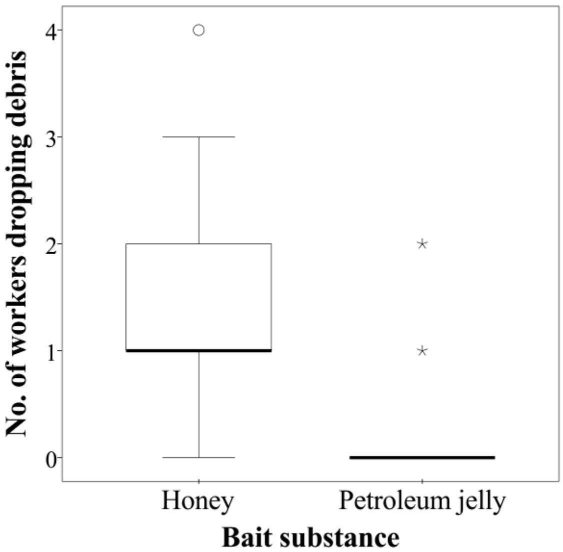

Fig. 4. The number of foraging workers of *Aphaenogaster subterranea* serving as debris droppers in the presence of the two types of bait substances. Boxes indicate the interquartile range; horizontal lines in the boxes indicate the medians; whiskers include all points to 1.5 times the interquartile range; open circles indicate outliers; asterisks indicate extreme outliers.

The types of tools used by foraging workers of *A. subterranea* varied somewhat from colony to colony. Particles of soil and easily movable, broken fragments of plant materials (e.g., bits of pine needle, cone and bark) were used most commonly, which were collected directly from the side of the baits. Tools were mostly carried by single workers, although in some cases, the larger, food-soaked items were transported cooperatively by two workers.

Discussion

Contrary to the members of the subfamilies Formicinae and Dolichoderinae, which possess a greatly distensible crop and a highly modified proventriculus allowing them the storage of large volumes of liquid food (Eisner and Brown 1958, Davidson *et al*. 2004), *Aphaenogaster* species, like other members of the subfamily Myrmicinae, lack these adaptations. In the case of *Aphaenogaster rudis*, for instance, the quantity of liquid food carried by an ant is only 10% of its original body weight (Fellers and Fellers 1976), while in the case of the syntopic formicine species, *Prenolepis imparis*, the extent of weight gain could reach an average of 130-200% (Lynch *et al*. 1980). In addition, the members of some genera in the subfamily Myrmicinae (e.g., *Aphaenogaster*, *Messor*, *Pogonomyrmex*) perform no trophallaxis (Agbogba 1985), a process by which other ant species exchange liquid food stored in their crops between members of a colony through regurgitation (Hölldobler and Wilson 1990). Tool use, therefore, may have evolved in these species to compensate for their inability to ingest and carry large volumes of liquid food and share it through trophallaxis with other colony members remaining in the nest. During this behaviour, foraging workers drop debris (e.g., particles of soil, bits of leaf, etc.) into the liquid food, and then transport the food-soaked tools back to the nest, where other workers lick the food from them (Fellers and Fellers 1976, Agbogba 1985).

This particular type of behaviour has been documented for eight species of the genus *Aphaenogaster* (Fellers and Fellers 1976, Tanaka and Ono 1978, Fowler 1982, McDonald 1984, Agbogba 1985, Cerdá *et al*. 1988, Banschbach *et al*. 2006), including *A. subterranea*, although in the case of the latter, only in laboratory colonies (Agbogba 1985). As was pointed out by Fellers and Fellers (1976) and McDonald (1984), this behaviour may have evolved from the tendency shown by many ant species to cover immovable, disagreeable substances (i.e., that present a potential hazard of drowning or entanglement to workers) near the nest with various types of debris particles, sometimes in sufficient amount to bury them completely (Wheeler 1910). This may explain why debris dropping behaviour is released more readily by the lower viscosity of the food (Tanaka and Ono 1978).

While in the study of Banschbach *et al*. (2006), *A. rudis* placed debris on 63-94% of the liquid food baits that it visited, debris dropping by *A. subterranea* was observed in all cases at honey baits, without any exception, in this study. Debris dropping usually began shortly after the baits were discovered, even if the tool-using workers had to crawl over the backs of feeding workers surrounding the food. The bits of debris were first placed around the periphery of the honey droplets, but subsequently building inwards until their entire surface was covered.

Similarly to other members of its genus, the tool-using behaviour of *A. subterranea* consisted of three distinct components (i.e., dropping, adjusting and transporting tools) that were usually performed by different individuals. In one case, however, a worker was observed that did not drop the carried tool item into the food, but started to dip it, and then immediately transported it away. Such a particular form of tool-using behaviour has not been documented even in the case of the well-studied *A. rudis* (Banschbach, pers. comm.), which raises the question of whether this behaviour represents a species-specific trait or its occurrence is too rare to be detected by similar studies.

Contrary to the fact that the number of workers manipulating tool items was positively correlated with the number of workers performing other activities, the proportion of tool-using workers constituted only a small fraction of the total number of workers that were observed at baits. This is

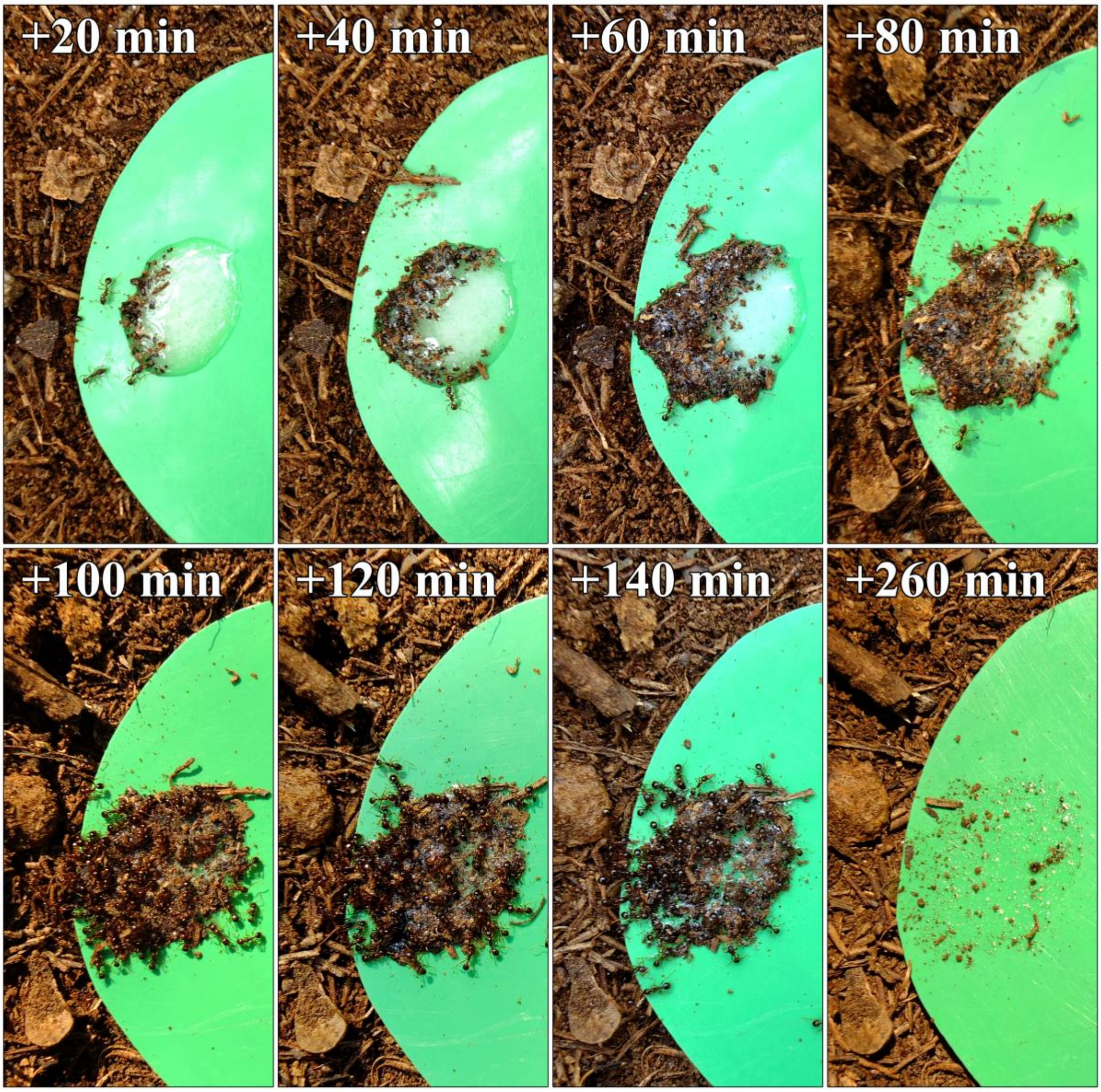

Fig. 5. Time course of honey removal by the tool-using workers of *Aphaenogaster subterranea* following the placement of baits.

consistent with the study of Banschbach *et al*. (2006), who demonstrated that tool-use represents a specialized task performed by a small subset of foraging workers of *A. rudis*, regardless of the size of the colony. The efficiency of the tool-using workers of *A. subterranea* was well shown in the case of the more active colonies, where tool-using workers, despite their small number, were able to transport almost all of the food available from the bait back to the colony in only a few hours (Fig. 5).

After a short searching time, the foraging workers of *A. subterranea* that served as debris droppers picked up tools that were nearest to the baits, and were the most easily movable. As was demonstrated in laboratory colonies of *Aphaenogaster famelica* and *A. rudis*, tool-using workers did show preference for certain tool items, which may be related to the ease of their manipulation or to the amount of food that can be absorbed or adhere to their surface (Fellers and Fellers 1976, Tanaka and Ono 1978). Nevertheless, in the natural habitats of *Aphaenogaster* species, the occurrence and availability of different potential tool items may also be important factors (Fellers and Fellers 1976).

One of the major adaptive advantages of tool use in retrieving food is that foraging workers are capable to transport much larger quantities of liquid food by tools than by direct, internal transport. For instance, by using tools, a worker of *A. rudis* is able to carry an amount of food approximately equalling its body weight (Fellers and Fellers 1976), while the amount of food carried by a worker of *A. famelica* is about 1.5-3.5 times its body weight (Tanaka and Ono 1978). The foraging activity of tool-using workers, and consequently the amount of food transported back to the colony, however, can be influenced by factors such as the size of the colony (McDonald 1984, Banschbach *et al*. 2006), the food demands of the colony (McDonald 1984, Barber *et al*. 1989, Banschbach *et al*. 2006) and the presence/absence of the foundress queen (Agbogba 1985).

In addition to a more effective utilization of liquid food, tool-use may increase the ability of *Aphaenogaster* species to compete more successfully with other ant species. By using tools, foraging workers do not need to spend a considerable time at the food source, so they can minimize interference with behaviourally dominant ant species that actively exclude subordinate species from food sources. For instance, in the study of Fellers and Fellers (1976), the workers of *A. rudis* dropped tools into the liquid food even in the presence of dominant ant species, and then returned later to retrieve the food-soaked tools once the dominant species leaved, thereby taking a lower risk than in the case of continuous feeding. In addition to other strategies employed by subordinate ant species (e.g., enhanced ability to find food sources, high thermal tolerances, avoidance behaviour, etc.), tool use may represent another method that allows these species to utilize food sources from which they would be otherwise excluded (Fellers and Fellers 1976). Furthermore, debris dropping may discourage other ants from visiting food sources that had been previously colonized by the tool-using species (Fowler 1982, Banschbach *et al*. 2006.). Since *A. subterranea* can be considered as an ecologically dominant species in the study habitat, being capable of monopolizing most of the baits (Lőrinczi, not published), the above discussed "stealthy behaviour" exhibited by the tool-using workers of *A. rudis* was not observed either in the present or in previous studies. Nevertheless, similarly to *A. rudis*, the foraging workers of *A. subterranea* began debris dropping even in cases when other species were present at the baits. Furthermore, in another study, *A. subterranea* was observed to be able to protect honey baits that had been fully covered with bits of debris against highly aggressive species like *Liometopum microcephalum* (Lőrinczi, pers. obs.).

At more than half of the baits, the foraging workers of *A. subterranea* dropped debris into the petroleum jelly, however, at a much lower intensity and quantity than in the case of honey. In the field study of McDonald (1984), a similar reaction was observed for *Aphaenogaster albisetosa*, whose workers regularly dropped pebbles and sand not only into honey water, but into distilled water, however, only up to a few meters from their nests. In contrast, in laboratory colonies of *Aphaenogaster senilis* and *A. subterranea* (Agbogba 1985), as well as *A. rudis* (Banschbach *et al*. 2006), workers were never observed dropping debris into non-food substances such as water or petroleum jelly, despite the proximity of these substances to their nests. This suggests that debris dropping as a general response to non-food viscous liquids that present a potential hazard of drowning or entanglement to workers may be highly species and/or context dependent.

Of course, the question arises when and how frequently do *Aphaenogaster* species exhibit tool use under natural conditions. Banschbach *et al*. (2006) found that potential tools (e.g., pieces of leaf and bark, clumps of dirt, etc.) represented a small, but non-negligible percentage of the items carried by the workers of *A. rudis* returning to their nests while no artificial food sources were available to the ants. Furthermore, in the laboratory experiments of Fellers and Fellers (1976) and Agbogba (1985), the workers of different *Aphaenogaster* species used tools to gather the body fluid of dead arthropods in the same way they had with the jelly or honey. All of these findings suggest that this particular form of behaviour is exhibited not only in the presence of artificial carbohydrate-rich food sources (e.g., honey water) and/or under laboratory conditions, but is an integral part of the natural foraging strategy of these species.

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