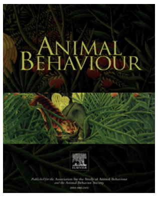
Animal Behaviour 123 (2017) 207–216

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Tool selection during foraging in two species of funnel ants

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ARTICLE INFO

Article history:
Received 30 April 2016
Initial acceptance 23 May 2016
Final acceptance 6 October 2016

MS. number: 16-00383R

Keywords:
ants
Aphaenogaster
food transport
foraging
tool use

Tool use by nonhuman animals has received much research attention in the last couple of decades. Nevertheless, research has focused mostly on vertebrates, particularly primates and corvids, even though tool use has also been documented in insects. One of the best documented examples involves ants using debris (e.g. sand grains, mud, leaf fragments) to collect and transport liquid food to their nest. However, little is known about the factors that determine the selection of materials to be used as tools. We investigated tool selection in two species of *Aphaenogaster* ants by giving them the choice between different kinds of potential tools (natural and artificial objects). Ant workers showed a clear preference for certain materials to be used as tool objects. Tool selection was also shaped by familiarity with the material as ants developed a preference for artificial tools with a good soaking capacity that cannot be found in their natural environment. Our results indicate that ants of this genus have evolved unique foraging strategies and show plasticity in their behaviour.

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Once considered unique to humans, tool use is now known to be widespread in the animal kingdom (Bentley-Condit & Smith, 2010; Shumaker, Walkup, & Beck, 2011). Moreover, in the last two decades our general understanding of the mechanisms underlying flexible tool use has greatly increased (Sanz, Call, & Boesch, 2013). Some species can make tools to meet specific task demands (e.g. Auersperg, Szabo, von Bayern, & Kacelnik, 2012; Bird & Emery, 2009; Sanz, Call, & Morgan, 2009), use multiple tools in succession to fulfil the subgoals required to complete a task (Martin-Ordas, Schumacher, & Call, 2012; Mulcahy, Call, & Dunbar, 2005; Wimpenny, Weir, Clayton, Rutz, & Kacelnik, 2009) or select appropriate tools depending on their physical attributes or functional properties (Bird & Emery, 2009; Chappell & Kacelnik, 2002; Manrique, Gross, & Call, 2010; Visalberghi et al., 2009).

Although these findings are concerned with vertebrates, mostly primates (chimpanzees, *Pan troglodytes*, orang-utans, *Pongo pygmaeus*, and capuchin monkeys, *Cebus apella*) and passerine birds (New Caledonian crows, *Corvus moneduloides*, rooks, *Corvus frugilegus*, woodpecker finches, *Camarhynchus pallidus*) (Sanz et al., 2013), tool use also occurs in invertebrates. For instance, a recently compiled catalogue reports about 50 cases of tool use in insects, involving 30 different genera (Bentley-Condit & Smith, 2010). However, little is known about the occurrence of flexible tool use in invertebrates. For instance, weaver ants use the silk produced by their larvae in nest building but this is not considered 'true' tool use because ants use an animate object (Pierce, 1986). Antlions and wormlions throwing out sand to make small prey fall inside their conical pits does qualify as tool use. Although this behaviour is stereotyped, it is not completely fixed: antlions modify the characteristics of their trap in line with hunger level, prey availability, predation threat and other environmental conditions such as light and temperature; however, the influence of experience upon this flexibility is unclear (Scharf, Lubin, & Ovadia, 2011). Antlions and wormlions also prefer specific substrates for pit building or ambushing prey (Devetak & Arnett, 2015). The use of pebbles to close burrows containing eggs and prey in some apoid wasps (*Ammophila*, *Sphex*) is flexible because it requires the selection of suitable pebbles (Evans & Eberhard, 1970).

One of the best documented examples of tool use by insects involves using debris to transport food by some species of ants including the harvester ant *Pogonomyrmex badius* (Morrill, 1972),

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http://dx.doi.org/10.1016/j.anbehav.2016.11.005
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Solenopsis invicta (Barber, Ellgaard, Thien, & Stack, 1989) and several species of *Aphaenogaster* (Agbogba, 1985; Fellers & Fellers, 1976; McDonald, 1984; Tanaka & Ono, 1978), all belonging to the subfamily Myrmicinae. Many of the species from this subfamily are characterized by a very chitinous gaster (abdomen) and by the lack of a distensible crop, which prevents the transport of large amounts of liquid food inside their bodies, a feature very common in other subfamilies, such as Formicinae or Dolichoderinae (Davidson, Cook, & Snelling, 2004; Hölldobler & Wilson, 1990). Furthermore, some myrmicine genera, namely *Aphaenogaster*, do not perform trophallaxis (Delage & Jaisson, 1969; i.e. mouth-to-mouth exchange of liquid food, also common in other subfamilies) and so the foragers of these species cannot exchange liquids stored in their crops with in-nest workers performing other tasks, such as feeding the larvae. The characteristic anatomy of the digestive tract in myrmicine ants, in particular an absence of an expandable crop, may have favoured the evolution of tool-using behaviour, which allows for efficient gathering, transport and sharing of liquid food (Fellers & Fellers, 1976; Tanaka & Ono, 1978).

When foragers of these myrmicine species encounter liquid food sources (e.g. fruit pulp, body fluids of dead arthropods) they drop debris of various kinds (e.g. sand grains, soil particles, leaf fragments) into the food source and then transport the food-soaked debris back into the nest. Furthermore, some evidence suggests that these ants do not drop debris into nonfood substances (Agbogba, 1985; Banschbach, Brunelle, Bartlett, Grivetti, & Yeamans, 2006). Tool-assisted food transport has been observed in both field and laboratory experiments with artificial baits (Agbogba, 1985; Banschbach et al., 2006; Barber et al., 1989; Fellers & Fellers, 1976; Fowler, 1982; Lőrinczi, 2014; McDonald, 1984; Morrill, 1972; Tanaka & Ono, 1978). Ants use as tools different objects found near the food source including mud clods, leaf fragments, pine needles, sand grains or any particles of a suitable size (Banschbach et al., 2006; Fellers & Fellers, 1976; Lőrinczi, 2014; Morrill, 1972; Tanaka & Ono, 1978). So far, however, only one comprehensive study has been carried out on tool selectivity in these ants (Tanaka & Ono, 1978). Other studies have reported limited observations that might indicate selectivity in use of tools in *Aphaenogaster* species (e.g. Banschbach et al., 2006; Fellers & Fellers, 1976; Lőrinczi, 2014; Morrill, 1972).

This putative material selectivity is important because it may indicate that ants choose materials flexibly, something that has been mainly documented in vertebrates. However, little is known about the factors that determine ants' preference for various materials as suitable tools for liquid transport. The aim of this study was to comprehensively investigate material selectivity in liquid food transport in two *Aphaenogaster* ant species in the laboratory to assess their flexibility and establish a possible link with the literature on tool use in vertebrates. We adopted St. Amant and Horton's (2008, p. 1203) definition of tool use, which is followed also by Bentley-Condit and Smith's (2010): ‘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’. We chose this definition instead of Beck's (1980) or Pierce's (1986) because it provided a good balance between specificity and generality and, crucially, it fully captured the behaviour that we investigated here.

We confronted ants with a liquid food source away from the nest and a set of natural or artificial (novel) objects with different weight/soaking properties. One might expect that tools with more efficient soaking properties would be preferred over alternative choices. Additionally, we expected that ants would preferentially drop debris in nutritious baits. The presentation of natural objects allowed us to link this study with previous ones while the inclusion of the artificial objects allowed us to explore the ants' flexibility in learning to use the most efficient novel materials.

METHODS

Study Species and Housing

We studied two monogynous Mediterranean ant species belonging to the subfamily Myrmicinae, *Aphaenogaster subterranea* and *Aphaenogaster senilis* (Czechowski, Radchenko, Czechowska, & Vepsäläinen, 2012; Stukalyuk & Radchenko, 2011). *Aphaenogaster subterranea* is a highly thermophilous species distributed in southern and central Europe (Czechowski et al., 2012; Seifert, 2007). It lives in moderately wet and warm deciduous and pine forests, and builds nests under stones, in the soil, litter or occasionally in fallen branches. Colony size can vary from several hundred up to 2000 workers (Czechowski et al., 2012; Seifert, 2007; Stukalyuk & Radchenko, 2011). *Aphaenogaster senilis* inhabits open, sunny locations such as forest edges, lawns, fields and sand dunes. The nests are built into the soil, often sheltered by stones. Workers forage individually mostly at the ground level, but they can occur on shrubs and trees. Since these habitats have scarce food sources, workers can cover large areas with the help of their long legs. Colony size can vary between a few hundred to a few thousand workers (Boulay et al., 2007).

Eight medium-sized colonies of *A. subterranea* (two queenright and six queenless, between 500 and 1500 workers) were collected in a black pine forest near the village of Litér (Hungary) and kept under standard conditions (temperature 24 ± 4 °C; relative humidity 42–43%; 12:12 h light:dark cycle) in the laboratory. Together with some material coming from the original habitat (soil, dried pine needles and leaf fragments), the colonies were kept in plastic boxes (44 × 31 cm and 23 cm high) with their cover cut in a circular shape (diameter 15 cm) and covered with a fine-wired metal mesh for ventilation and easy moistening of the nest. Every box containing a colony was connected with a 10 cm long plastic tube to an arena (60 × 30 cm and 15 cm high). They were watered daily, and fed every second day with a commonly used artificial diet (Bhatkar & Whitcomb, 1970) in a distant location of the foraging arena. During the experimental period the colonies were not fed, to increase motivation for food found on the baits. Water was always provided.

Three queenright colonies of *A. senilis* (colony size 500–1500 workers) were collected at Banyuls-sur-Mer (France) in a sandy area and kept in the laboratory under standard conditions (temperature 24 ± 4 °C; relative humidity 50–60%; 12:12 h light:dark cycle). They were housed in artificial nests, each consisting of a cylindrical plastic box (diameter 12.5 cm) with regularly moistened plaster floor, and a hole giving access to the foraging area, which was represented by the space left in a larger plastic box (18 × 25.5 cm and 7.7 cm high) containing the circular nest. The standard diet for each colony consisted of five dead crickets, *Acheta domestica*, and about 5 g of apple/honey mix twice a week. During the experimental period, to increase motivation for food, colonies were fed with only three crickets and 2 g of apple/honey mix (twice a week); water was always provided ad libitum.

Experimental Set-up

Ant colonies were given food baits and different types of potential tools in the foraging arena (Figs. 1 and 2). The methodology used and described below is slightly different for *A. subterranea* and *A. senilis* because this study is the combined output of two initially

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