Animal Behaviour 91 (2014) 53–59

Contents lists available at ScienceDirect

Animal Behaviour

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

Cues or meaningless objects? Differential responses of the ant *Formica cinerea* to corpses of competitors and enslavers

István Maák [a,*], Bálint Markó [b,*], Katalin Erős [b,c], Hanna Babik [d], Piotr Ślipiński [d], Wojciech Czechowski [d]

[a] Department of Ecology, University of Szeged, Szeged, Hungary
[b] Hungarian Department of Biology and Ecology, Babes-Bolyai University, Cluj-Napoca, Romania
[c] Department of Evolutionary Zoology, University of Debrecen, Debrecen, Hungary
[d] Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland

ARTICLE INFO

Article history:
Received 6 July 2013
Initial acceptance 5 August 2013
Final acceptance 14 January 2014
Available online 27 March 2014
MS. number: 13-00558R

Keywords:
aggression
ant
competition
corpse
Formica fusca
Formica polyctena
Formica sanguinea
recognition
prophylactic behaviour

Group living involves major health risks, since it facilitates the spread of pathogens and parasites among members. To counteract this negative effect, social insects, such as ants, adopt several social defensive strategies, one of the most widespread being the collective disposal of corpses often outside the nest, which represent potential sources of infection. Corpses might even be used during interspecific conflicts to inhibit the activity of the attacked nest or they could be consumed as food. As intra- and interspecific relationships are manifold and often vary in terms of fitness consequences for the interacting species, it can be hypothesized that responses to corpses of different origin can vary. Scattered or piled up corpses of different ant species could act as cues for foragers, signalling the presence of other species, and triggering appropriate responses: alarm, retreat or foraging. We examined the reactions of the ant *Formica cinerea* under natural conditions to corpses of co-occurring *Formica* species. *Formica cinerea* responded differentially to corpses of different origin. Those of the territorial *Formica polyctena* and the slave-maker *Formica sanguinea* elicited more aggression and their corpses were removed sooner than other dead bodies. The majority of corpses were carried inside the nest, with the exception of *Formica fusca* corpses, which may signify the lack of specific interest in this species. The removal of nestmate and foreign conspecific corpses could be explained through social prophylaxis, and that of superior competitors additionally by conflict avoidance and/or by food supplementation. Based on our results, for ants corpses are not meaningless objects scattered around ant nests, but cues that carry information that trigger different behavioural reactions.

A social lifestyle, its advantages notwithstanding, can pose many health risks, as the intense relationships among constituent members of a group can assist the spread of pathogens and parasites (Choe & Rust, 2008; Graham, 2007; Soeprono & Rust, 2004; Wiltz, Suiter, & Gardner, 2010). To counteract these negative effects, a plethora of social and individual behavioural strategies have evolved in social animals, including ants: frequent self- and allogrooming, pathogen and parasite recognition and avoidance, recognition and social rejection of infected individuals, self-exclusion of infected workers, etc. (Bos, Lefèvre, Jensen, & D'Ettore, 2012; Castella, Chapuisat, & Christe, 2008; Diez, Deneubourg, & Detrain, 2012; Evans, Elliot, & Hughes, 2011; Graham, 2007; Heinze & Walter, 2010; Oi & Pereira, 1993; Renucci, Tirrard, & Provost, 2011; Wilson, Durlach, & Roth, 1958). One of the most efficient methods of social prophylaxis in social insects is the collective disposal of accumulated waste and necrophoresis, the removal of dead colony members and the formation of refuse piles or so-called cemeteries (Ballari, Farji-Brener, & Tadey, 2007; Chouvenc, Robert, Sémon, & Bordereau, 2012; Diez, Le Borgne, Lejeune, & Detrain, 2013; Evans, Groden, & Bischoff, 2010; Farji-Brener & Sasal, 2003; Graham, 2007; Jost et al., 2007; Oi & Pereira, 1993; Renucci et al., 2011; Theraulaz et al., 2002; Wilson et al., 1958). These refuse piles are usually located far from the nest (Graham, 2007; Oi & Pereira, 1993; Renucci et al., 2011), for example in extreme cases, as in territorial wood ants, corpses could even be disposed of several metres from the nest along the territory border (Dlussky, 1965). Some species, though, scatter the corpses and the refuse around the nests without forming well-contoured piles (e.g.

* Correspondence: I. Maák, Department of Ecology, University of Szeged, Közép fasor 52, H-6726 Szeged, Hungary and B. Markó, Hungarian Department of Biology and Ecology, Babes-Bolyai University, Clinicilor 5-7, 400006 Cluj-Napoca, Romania.
E-mail addresses: bikmakk@gmail.com (I. Maák), mbalint@biolog.ubbcluj.ro (B. Markó).

http://dx.doi.org/10.1016/j.anbehav.2014.02.014
0003-3472/

Banik, Biswas, Karmakar, & Brahmachary, 2010; Diez, Deneubourg, Hoebeke, & Detrain, 2011; Diez et al., 2012; Howard & Tschinkel, 1976), while in other cases, dead nestmates are stored in special 'burial chambers' within nests (e.g. Bot, Currie, Hart, & Boomsma, 2001; Chouvenc et al., 2012; Czechowski, 1976; Renucci et al., 2011; Staeger, 1926).

It is generally assumed that the appearance of ant corpses poses a danger to ants. Corpses could be sources of infection; thus ants may reject suitable nesting sites if nestmate corpses are nearby (Franks, Hooper, Webb, & Dornhaus, 2005; Renucci et al., 2011), or even avoid foraging sites when refuse dumps are present (Ballari & Farji-Brener, 2006; Farji-Brener & Sasal, 2003). Probably because of their inhibiting nature, bodies of dead ants can also be used in conflict situations. Czechowski (1990) observed that in the territorial *Formica exsecta*, corpses of this species are piled up on the edge of the territory during an intraspecific conflict, probably acting as territorial signals. Gordon (1984) also found that middens serve as a territorial signal for *Pogonomyrmex badius*, as their removal causes interspecific conflicts among neighbours in the nest area. The slave-maker *Formica sanguinea* is known to transport its corpses to the entrance of a nest of the slave species *Formica cinerea* when raiding it (Czechowski, 1977). Similar behaviour has been observed in other ant species as well (Czechowski, 1985; Czechowski, Markó, & Godzińska, 2009). The authors of these studies (Czechowski, 1977, 1985; Czechowski et al., 2009) reached the conclusion that, while raiding, corpse-carrying activity of the aggressors has an inhibitory or intimidating effect on the activity of their adversaries.

In addition to being signals of danger, corpses can also constitute potential food sources for some ant species (Czechowski, 2008; Czechowski, Markó, & Radchenko, 2008; Howard & Tschinkel, 1976; Wilson et al., 1958). In ants, predation on other ants is generally known both on the inter- and intraspecific level (e.g. Carroll & Janzen, 1973; Czechowski, 2002; Mabelis, 1979; Markó, Czechowski, & Radchenko, 2013); thus, it is not surprising that scavenging on ant corpses also occurs, similarly to some termite species, which consume fresh corpses (Kok-Boon, Beng-Keok, Kunio, Tsuyoshi, & Chow-Yang, 2012).

How could an ant tell a corpse from a living individual? The basic cues used by ants for nestmate and non-nestmate discrimination are hydrocarbons accumulated on the cuticle of ants constituting the so-called cuticular hydrocarbon (CHC) profile (see Martin & Drijfhout, 2009 for a review). There are certain components of the CHC (e.g. oleic acid and unsaturated fatty acids) that become dominant on the cuticular surface after death that are responsible for the so-called 'corpse smell' of decaying insects (Choe, Millar, & Rust, 2009; Chouvenc et al., 2012; Diez, Moquet, & Detrain, 2013; Wilson et al., 1958). This typical smell arises about 50 min after the death of the individual (Choe & Rust, 2008; Howard & Tschinkel, 1976; Wilson et al., 1958), and it persists for a long period (Diez, Moquet, et al., 2013); for example, Choe et al. (2009) did not find any major difference in the reaction of ants towards corpses 1 and 24 h old. In addition, the CHC profile of corpses retains other specific information that allows the differentiation between corpses of nestmate or non-nestmate conspecifics or even corpses of competitors (Bos, Guerrieri, & D'Ettore, 2010; Cournault & de Biseau, 2009; Diez, Moquet, et al., 2013; Renucci et al., 2011).

One could easily assume that corpses should be handled alike in ants irrespective of their origin. Since the outcome of various interactions among ants may have serious fitness consequences, we could expect that besides precise self–nonself recognition, appropriate discrimination could apply to corpses as well, as they may indicate the proximity of a potential enemy. The behavioural response to dead bodies of different origin could vary, as the appearance of some, such as those of territorial ants or rivals, may signify a threat, thus eliciting aggression and/or inhibiting activity (see e.g. Czechowski et al., 2009; Diez, Moquet, et al., 2013), while others, such as food items, may elicit positive reactions, and some even none. Scattered or piled up corpses around ant nests may act as important information carriers for any foraging ant, and the emergence of rapid and appropriate responses to these cues would be evolutionarily advantageous (Renucci et al., 2011). The quick alarm reaction to an imminent raid, the avoidance of the vicinity of a superior competitor's nest, or the quick recognition of potential food sources are of vital importance for the individual, and ultimately for the ant colony. Such variations in the response of ants to different types of corpses have already been observed in laboratory experiments (Diez, Moquet, et al., 2013; Renucci et al., 2011). However, little is known about the response of ants when meeting such 'cues' in the field. We hypothesized that (1) the responses of a given species to a set of corpses of different origin could vary, and (2) this variation could be determined by the nature of the relationships between species. These variations could manifest themselves (a) in behavioural responses (e.g. neutral versus aggressive behaviour) elicited by corpses of different origin, but also (b) in differences in the activity of workers (e.g. recruitment) at dead bodies. Corpse removal activity (if any) may also vary (c) in rate and (d) direction: while some corpses may be taken rapidly inside the nest and probably consumed, others, for example those of nestmates and foreign conspecifics, as potential casualties of any infection, may be taken far from the nest and, eventually, piled up.

There has never been a comprehensive field experiment specifically designed to test reactions of ants to corpses of different origin, thus testing the information carrier potential of dead bodies. To test the above hypothesis, we conducted a series of field experiments with *F. cinerea* ant species as a study organism. There are a few field observations on the response of this species to ant corpses (Czechowski, 1977; Czechowski et al., 2009), and, in addition, a plethora of data is available on the nature of its interspecific relationships (e.g. Czechowski & Markó, 2005; Czechowski & Rotkiewicz, 1997; Markó & Czechowski, 2012). In the course of our study we investigated the responses of *F. cinerea* workers to corpses of different origin, all belonging to co-occurring ant species with documented relationships with *F. cinerea*: foreign conspecific, slave-maker, dominant territorial and submissive ant species.

METHODS

Study Species and Site

Formica (*Serviformica*) *cinerea* is a typical ant species of sunny, mostly sandy habitats, from coastal and inland dunes to light pine forests or towns in temperate Europe and West Siberia. It lives largely by way of predation and scavenging, while also feeding on honeydew. Its competitive hierarchical status is context dependent, but it is mostly categorized as an aggressive species (Markó & Czechowski, 2004, 2012).

The study was carried out in the northeast part of the Kampinos National Park, Poland in August 2011. The Kampinos NP is located in the valley of the Vistula River and represents a mosaic of habitats, ranging from marshlands to sandy dunes, although mixed pine forests of *Vaccinio-Piceetea* prevail. The study nests were located within a forest clearing of just under 1000 m^2 near Palmiry village (52.3638N, 20.7786E, 82 m above sea level). The study site was surrounded with a mature Scots pine, *Pinus sylvestris*, forest mixed with some birches, *Betula* spp., and other young trees such as rowans, *Sorbus aucuparia*, and firs, *Abies alba*. The sandy soil was covered mostly by patches of moss and lichen, and locally with sparse herbaceous vegetation.