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A comparative analysis of precision rescue behaviour in sand-dwelling ants

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A sand-dwelling Mediterranean ant, *Cataglyphis cursor*, recently was discovered to engage in two new forms of rescue behaviour, behavioural patterns that require would-be rescuers to recognize what, exactly, holds nestmates in place. That is, when sand digging and limb pulling, two well-known forms of rescue in ants, did not result in release of victims ensnared with nylon thread and partially buried beneath the sand, rescuers next began to transport sand away from the snare and to direct their behaviour to the snare in particular, biting and tugging at the snare itself. To determine whether these new forms of precisely directed rescue behaviour, as well as their exclusive delivery to nestmates, as in *C. cursor*, were characteristic of other ants occupying similar ecological niches, we conducted experiments with five sand-dwelling Mediterranean ant species: *Cataglyphis floricola*, *Lasius grandis*, *Aphaenogaster senilis*, *Messor barbarus* and *Messor marocanus*. Our experiments revealed the full range of rescue behaviour, including snare biting and sand transport, in two species, *C. floricola* and *L. grandis*. Both species directed rescue exclusively towards nestmates, treating other individuals, even conspecifics, with aggression, thus highlighting the ants' discriminative capacities. Differences in the performance of rescue behaviour between these and the remaining species mirror differences in their ecology, including the threat of predatory antlions. Finally, because this precisely directed and exclusively delivered rescue behaviour in ants resembles behaviour that has been labelled empathy in rats, our results demonstrate that what can appear to be complex, cognitively motivated behaviour might come about through much simpler mechanisms.

Recently, Nowbahari et al. (2009) demonstrated that *Cataglyphis cursor*, a common sand-dwelling Mediterranean ant, is capable of performing forms of rescue behaviour that had not been previously reported, despite a literature that dates as far back as Belt's (1874) monograph on ant behaviour. That is, when *C. cursor* ants were presented with experimentally ensnared nestmates held in place with nylon thread, ants not only engaged in sand digging and limb pulling, both familiar forms of rescue behaviour in ants (e.g. Lafleur 1940; Wilson 1958; Markl 1965; Blum & Warter 1966; Spangler 1968; Hangartner 1969), but also somehow were able to detect what, exactly, held victims in place: when digging and pulling did not result in the victim's release, ant rescuers next transported excavated sand away from the victim's body, exposed the nylon thread, and then immediately bit and tugged at the snare directly. Carefully aimed, snare biting never was misplaced, even though the snare was in direct contact with the victim's body.

Nowbahari et al. (2009) argued that sand transporting and, especially, snare biting might require slightly more complicated mechanisms than simple sand digging and limb pulling. That is, digging and pulling require only that ants are alerted by a nestmate's alarm signal, follow the sensory gradient to the source, and then commence digging and pulling once they make contact with the victim, a series of behaviour patterns easily explained by simple releasing mechanisms. However, it is difficult to see how these same simple mechanisms could guide rescuers to the precise location of whatever object is holding the victim in place while ignoring other 'non-ant' objects nearby, enable them to expose it further by transporting sand away from this object, and then finally target their bites to the object itself, transporting additional sand as necessary. In addition, because *C. cursor* directed this rescue behaviour only towards nestmates, never even approaching ants belonging to nearby colonies of the same species, the 'call-for-help' signal, in this species at least, necessarily contains a component unique to each colony. Such precisely directed and exclusively

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targeted rescue behaviour would be expected to evolve only when members of a particular species faced risks of possible entrapment, and the benefits of releasing conspecifics exceeded what appear to be particularly high costs of engaging in rescue behaviour.

Although the risks of entrapment would not be limited to sand-dwelling ants like *C. cursor*, sand-dwelling species are likely candidates for several reasons. The experiments with *C. cursor* were prompted by field observations in which forager ants often attempted to rescue nestmates that had been partially buried under collapsing sand and debris (Nowbahari et al. 2009). Yet another potential opportunity for rescue occurs when ants fall into the traps of pit-digging larval antlions (Neuroptera: Myrmeleontidae). Antlions' pit traps are found in some of the same habitats as sand-dwelling ants and, although antlions prey upon many different arthropods, ants are one of the most common prey items (Griffiths 1980; Lucas & Brockmann 1981; Botz et al. 2003; Mencinger-Vračko & Devetak 2008). Antlions' pit traps, dug in loose sandy soils (Devetak et al. 2005), are constructed in such a way to funnel prey to the centre of the pit, where the predator is waiting; however, prey sometimes are able to cling to the sides of pits for short periods of time, despite attempts by antlions to dislodge their prey by sand tossing (Hollis & Guillette 2011; Hollis et al. 2011). Thus, rescue behaviour also may be an important antipredator defence. Indeed, in several field experiments with *Formica* workers reared as slaves, Czechowski et al. (2002) demonstrated that enslaved ants immediately rushed to the aid of heterospecific nestmates captured by antlions and began to engage in sand-digging and limb-pulling behaviour.

Despite its obvious benefits, rescue behaviour entails costs that, for some ant species, may be too high to pay. Rescue behaviour not only is an energetically costly behaviour that prevents individuals from devoting time to other important tasks, but also poses large risks to rescuers (Nowbahari & Hollis 2010). For example, rescuers themselves may become buried under sand as they attempt to aid an entrapped nestmate. In addition, because some predators, including antlions, are capable of seizing multiple prey items in rapid succession, rescuers risk capture. Because of its costs, then, we would predict that not all ant species are able to engage in rescue behaviour. Thus, one goal of this study was to determine how common the phenomenon of precisely directed rescue behaviour is in ants, as well as to establish whether, like *C. cursor*, foragers rescue only nestmates.

A second, related goal was to determine what might be some of the ecological variables that promote rescue in ants. To address both objectives, we conducted a comparative analysis of rescue behaviour in five species of sand-dwelling Mediterranean ants representing two subfamilies: *Lasius grandis* and *Cataglyphis floricola* (bicolour morph) from the subfamily Formicinae; and, *Aphaenogaster senilis*, *Messor barbarus and Messor marocanus* from the subfamily Myrmicinae. Because *C. floricola* not only inhabits the same loose sandy soils as *C. cursor*, but also lives in close proximity to pit-digging antlions, we expected that *C. floricola* would be likely to show the same kinds of rescue behaviour as its close relative, *C. cursor*. At the other end of the spectrum, *Messor* species inhabit more compact soils than do *Cataglyphis*, and thus are probably less likely to become trapped by collapsing sand. In addition, *Messor* foragers form ant trails, long lines of individuals following marked trails leading to food (López et al. 1993; Hölldobler & Wilson 2009), making accidental encounters with antlion pits, or any other dangerous situations, far less likely.

Yet another goal of this study was to shed light on the phenomenon of rescue behaviour more generally. Although anecdotes of rescue in nonhuman animals abound in the popular media, the scientific literature contains only two experimental analyses of rescue behaviour, one in ants (Nowbahari et al. 2009) and one in rats (Bartal et al. 2011). Interestingly, the report of rescue behaviour in rats describes behaviour analogous to what Nowbahari et al. (2009) observed in ants. Although the authors themselves do not use the word 'rescue' to describe rats' behaviour, preferring the term 'empathy' instead, our research with ants raises questions about the necessary and sufficient conditions for interpreting behaviour as empathic. That is, if ants respond to conspecifics in ways that appear nearly identical to those of a mammal, then future experiments exploring empathy in animals will need to include control groups that help scientists to distinguish between analogous behaviour involving different mechanisms (Vasconcelos et al. 2012).

METHODS

Subjects and Materials

We observed the behaviour of five sand-dwelling Mediterranean ant species in the field between April 2010 and June 2011 in response to four kinds of test stimuli, namely a homocolonial nestmate, a heterocolonial ant, or a heterospecific ant held in place using a filter paper and thread snare, or an empty paper-and-thread snare in a control test. Only colonies that showed high activity levels and large numbers of foragers present on the surface near the nest entrance were chosen for study. All data were collected during ants' active period, either in the morning, at least 1 h after foragers had emerged from the nest but before ants retreated to the nest at midday, or later in the afternoon, at least 1 h after foragers had re-emerged but before ants retreated to the nest near the end of the day. We observed one of the ant species, *M. barbarus*, in Argelès-sur-mer (Languedoc-Roussillon) with permission from Institut National des Sciences de l'Univers; we observed all four of the remaining ant species, *L. grandis*, *C. floricola*, *A. senilis*, and *M. marocanus*, in the Doñana Biological Reserve (Reserva Biológica de Doñana, RBD) in Southwestern Spain. All fieldwork in Doñana was formally approved by the ICTS-RBD program. Specimens of each species were returned to the laboratory to ensure correct identification (Bernard 1968; Tinaut 1991).

Filter paper snares were prepared in advance of all trials: using a sewing needle, a small loop (0.5–0.75 cm, depending on the test species) of two-ply cotton thread was inserted near one end of a strip (2 cm long × 1 cm wide) of clean filter paper; the ends of the thread were tied loosely underneath the paper and left hanging until needed in the field. Prepared snares were kept in a clean plastic box to avoid contamination and a clean snare was used for each test.

Procedure

The testing procedures were similar to Nowbahari et al. (2009) but adapted to field conditions where noted below. For homocolonial (nestmate) tests, the ant victim was chosen from amongst the foragers near the nest entrance, grasped with insect handling tweezers, gently inserted under the thread loop on the filter paper such that the thread encircled the victim's pedicel (waist), and then secured to the filter paper by pulling on the ends of the thread underneath the paper. A single knot held the victim in place. Next, the filter paper was trimmed to a length of approximately 1.0–1.5 cm (depending on species size) and the ends of the thread were clipped close to the knot such that no thread extended beyond the edges of the paper. For heterocolonial tests, the victim was chosen from a nearby colony of the same species, at least 30 m from the test colony, and tied to the filter paper as described above. Heterospecific tests were conducted in the same manner as heterocolonial tests, except that ant victims were chosen from colonies