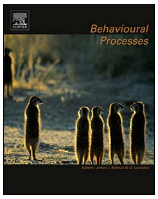
Behavioural Processes 144 (2017) 1–4

Contents lists available at ScienceDirect

Behavioural Processes

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



Pro-social behaviour of ants depends on their ecological niche—Rescue actions in species from tropical and temperate regions

Krzysztof Miler[a,*], Bakhtiar Effendi Yahya[b], Marcin Czarnoleski[a]

[a] *Institute of Environmental Sciences, Jagiellonian University, Poland*
[b] *Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Malaysia*

ARTICLE INFO

Keywords:
Ants
Antlions
Entrapment
Rescue behaviour

ABSTRACT

Some ants display rescue behaviour, which is performed by nearby nestmates and directed at individuals in danger. Here, using several ant species, we demonstrate that rescue behaviour expression matches predicted occurrences based on certain aspects of species' ecological niches. Rescue occurred in sand-dwelling ants exposed both to co-occurring antlion larvae, representing the threat of being captured by a predator, and to nest cave-ins, representing the threat of being trapped in a collapsed nest chamber. Rescue also occurred in forest groundcover ants exposed to certain entrapment situations. However, rescue never occurred in species associated with open plains, which nest in hardened soils and forage largely on herbaceous plants, or in ants living in close mutualistic relationships with their host plants. In addition, because we tested each species in two types of tests, antlion larva capture tests and artificial entrapment tests, we highlight the importance of accounting for test context in studying rescue behaviour expression.

1. Introduction

Altruism occurrence is of special interest in scientific inquiry (Pennisi, 2005). A type of altruistic (pro-social) behaviour, called rescue behaviour, is observed when a rescuer performs an act to lower a threat to an imperilled individual (Vasconcelos et al., 2012). Such behaviour has been described in several animal taxa. Rats have been observed to rescue other restrained rats (Bartal et al., 2011) and birds to rescue group members from death following entanglement (Hammers and Brouwer, 2017). However, the most common examples of rescue behaviour include those involving predatory threat to the endangered individual. Accordingly, humpback whales have been observed to interfere with predation by killer whales, allowing targeted individuals to escape (Pitman et al., 2017), whereas ants have been shown to carry their injured nestmates back to the nest after fighting to reduce after-combat mortality related primarily to predation by spiders (Frank et al., 2017). Indeed, ants are the most studied taxa regarding rescue behaviour occurrence (Hollis et al., 2015; Hollis, 2016).

To date, the majority of studies on rescue behaviour have been performed on sand-dwelling ants, which are known to be exposed to predation by antlion larvae and nest cave-ins, two agents that have likely contributed to the evolution of rescue behavioural patterns, making them especially prevalent in ants. Sand-dwelling ants can minimize the risk of predation by antlions by simply avoiding antlion aggregation zones and their pitfall traps (Gotelli, 1996; Morrison, 2004; Hollis et al., 2017), but even when a foraging ant stumbles into the trap, not all is lost if its nestmates come to rescue. Indeed, rushing into an antlion larva trap and acting to free a trapped nestmate has been observed in some species co-occurring with antlion larvae. Ant species of the genera *Cataglyphis*, *Formica* and *Lasius* (all belonging to the subfamily Formicinae) have been demonstrated to show clear rescue behaviour (Czechowski et al., 2002; Hollis and Nowbahari, 2013a; Miler, 2016), but it appears that ants from other subfamilies, i.e., Myrmicinae and Ponerinae, are also capable of some rescue behaviour (Hollis and Nowbahari, 2013a; Frank et al., 2017). The existence of rescue in distantly related ant species suggests that this behaviour is not phylogenetically constrained and that many ecological factors may contribute to its occurrence. It is likely that the evolution of rescue behaviour in ants was driven by a broad range of ecological factors that cause entrapment, e.g., collapsing or sticky objects (Hollis and Nowbahari, 2013a). Unfortunately, very little is known about how often and in which ecological contexts rescue behaviour has evolved in ants.

To advance our understanding of the evolution of rescue behaviour, we need to determine whether the elicitation of rescue actions varies among ant species that are naturally exposed to different risks and types of entrapment situations. To address this question, we studied the elicitation of rescue behaviour in six distantly related species of ants

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* Corresponding author at: Gronostajowa 7, 30-387 Kraków, Poland.
E-mail address: krzysztof.miler@uj.edu.pl (K. Miler).

http://dx.doi.org/10.1016/j.beproc.2017.08.010
Received 10 May 2017; Received in revised form 26 July 2017; Accepted 16 August 2017

Table 1
An expected gradient 1–4 in the risk of entrapment of foraging ants of different species. Each species inhabited a specific microhabitat in either a tropical (Borneo) or temperate (Poland) environment. The risk of entrapment was assessed based on a general knowledge of the biology of the studied ants and prior field studies that have identified the co-occurrence of the studied ants with antlion larvae and other agents that can lead to entrapment situations (e.g., being stuck in clay, organic debris or plant secretions).

The overall level of entrapment risk		1 (minimal)	2 (low)	3 (moderate)	4 (maximal)
Ecological niche		Ant-mutualistic plants	Open plains	Forest groundcover	Sands
Study region	Borneo	*Camponotus korthalsiae* (Formicinae)	*Anoplolepis gracilipes* (Formicinae)	*Iridomyrmex anceps* (Dolichoderinae)	–
	Poland	–	*Myrmica ruginodis* (Myrmicinae)	*Formica polyctena* (Formicinae)	*Formica cinerea* (Formicinae)
Risk of entrapment	Antlion	Very low	Very low	Very low	Very high
	Other agents	Very low	Low	High	Very high

originating from different microhabitats. Our study was conducted in tropical (Borneo) and temperate (Poland) regions spanning a wide spectrum of microhabitats with different exposures of the ants to entrapments. We considered six species of ants from four distinct niches while maintaining overlap in both regions in two of these niches (lack of corresponding microhabitats made this impossible for the other two). Each niche was scored with a value from 1 to 4 according to the overall risk of entrapment: (1) ant-mutualistic plants with minimal risk of entrapment (Borneo), (2) open plains with low risk of entrapment (Borneo and Poland), (3) forest groundcover with moderate risk of entrapment (Borneo and Poland), and (4) sands with maximal risk of entrapment (Poland). As detailed in Table 1, we predicted that the relative risk of entrapment caused by antlions vs other ecological agents differs among the studied ant species. On the lower end of our continuum, there are plant-mutualistic ants from a rainforest on Borneo (1) that would never face entrapment by any type of agent as they live exclusively on their palm trees (Edwards et al., 2010; Miler et al., 2016). On the other end of the continuum, there are sand-dwelling ants from a desert area in Poland (4) that frequently face different types of entrapment, including capture by antlion larvae (Czechowski et al., 2002a). Ants in open plains (2) or ants in forest groundcover (3) are never exposed to antlion predation, but they may be at some risk of other entrapment situations, e.g., being stuck in clay, organic debris or plant secretions (see, e.g., Lafleur, 1940; Krimmel and Wheeler, 2015). Our major expectation was that ants naturally exposed to any type of entrapment risk, regardless of phylogenetic affiliation, have evolved rescue behaviour, which would be demonstrated in our laboratory tests of the elicitation of rescue actions. Importantly, in each ant species, we employed two types of rescue behaviour tests: one with ants captured in pitfall traps built by antlion larva (antlion larva capture tests) and another with ants entrapped by physical agents, which mimicked entrapment by non-antlion causes (artificial entrapment tests). Rescue behaviour in ants has typically been studied in artificial entrapment tests (Nowbahari et al., 2009, 2012, 2016; Hollis and Nowbahari, 2013a; Duhoo et al., 2017), which are assumed to be relevant to the entrapment caused by antlion larvae (Hollis et al., 2015; Hollis, 2016). If ants do not discriminate between different contexts of entrapment, we would expect that both types of tests would produce similar results. This finding would agree with the assumption that the results of the artificial entrapment tests are generalizable to antlion entrapments in the field. In contrast, if the ecological context of entrapment matters, we would expect an inconsistency in the results between our two types of tests.

2. Methods

In Borneo, we collected ants in the vicinity of the Danum Valley Field Station (*Camponotus korthalsiae*, *Anoplolepis gracilipes*, and *Iridomyrmex anceps*, identified with a reference to Bolton's keys (Bolton, 1994, 2003)). Locally occurring antlion larvae (*Myrmeleon* sp.) were collected in sandy areas under buildings and were kept in a laboratory in plastic cups (7 cm in diameter, 8 cm high) filled with sieved sand that originated from their primary habitat. The tests were performed in July 2016 in a laboratory at the field station. To mimic natural conditions, the tests were conducted at temperatures between 30 and 32 °C and at a relative humidity of 70–90%. In Poland, we collected ants in the Błędowska Desert and surrounding areas, including the coniferous forest (*Myrmica ruginodis*, *Formica polyctena*, and *Formica cinerea*, identified based on Czechowski's and co-authors' key (Czechowski et al., 2002b)). Antlion larvae (*Myrmeleon bore*, identified following Badano and Pantaleoni (2014)), were collected from the Błędowska Desert, and they were kept in the same cups as those used in Malaysia, filled with sieved sand that came from their original habitat. Tests were performed in September 2016 in a laboratory at the Institute of Environmental Sciences in Kraków. To mimic natural conditions, the tests were conducted at temperature between 24 and 25 °C and at a relative humidity of 50–70%.

The tests of rescue behaviour performed in Borneo and Poland followed exactly the same protocol. Each day before noon, we collected active foragers from two distant colonies of one of the studied ant species, and in the afternoon, we examined the elicitation of rescue behaviour using the two test types (each ant species was tested on a separate day). In each antlion larva capture test, we dropped a single ant into the trap of an antlion larva, formed in a cup with sand. Immediately after an ant was captured, a nestmate ant was placed on the flat surface of sand around the trap. In each artificial entrapment test, we used the same cups as in the antlion larva capture tests, with no antlion larvae and fresh sand with a flattened surface. A single ant was tied by the petiole to a round piece of filter paper (diameter 1.5 cm) using a thin cotton thread (Nowbahari et al., 2009, 2012, 2016; Hollis and Nowbahari, 2013a; Duhoo et al., 2017). Then, the tied ant was placed inside the test cup and the filter paper was covered with a thin layer of sand, such that the ant stayed above the sand but was unable to move freely. As in the antlion larva capture tests, we then placed a nestmate ant into the cup, at a body-length distance from the entrapped individual. Each test began immediately after a potential rescuer was introduced to the cup and ended two minutes later. During this time interval, we recorded any overall signs of rescue behaviour (0/1 response) and measured the latency (in s) from the beginning of the test to the first episode of any type rescue behaviour (if it occurred). Ants were considered to engage in rescue actions when they were observed digging around the entrapped individual, pulling the limbs/antennae/mandibles of the entrapped individual, removing sand covering the entrapped individual, attacking antlion larvae (in the antlion larva capture tests), or biting the thread that was anchoring an entrapped individual (in the artificial entrapment tests). In total, we performed 25 tests of each type on each colony per species. No ant was used twice. Statistical analysis was performed in STATISTICA 12.5 (StatSoft, Poland). Our hypotheses concerned differences between species and test types; therefore, we pooled data from two colonies within each species. We used the Fisher exact test (FET) to compare the frequency of tests that recorded rescue behaviour between ant species. This analysis was performed separately for each test type. Data on the latency of rescue actions were analysed with the Kruskal-Wallis ANOVA (K-W ANOVA), and this analysis was limited to tests in which rescue behaviour was