Precision Rescue Behavior in North American Ants

Katherine Taylor, Interdisciplinary Program in Neuroscience and Behavior, Mount Holyoke College, South Hadley, MA, USA.

Allison Visvader, Interdisciplinary Program in Neuroscience and Behavior, Mount Holyoke College, South Hadley, MA, USA.

Elise Nowbahari, Laboratoire d’Éthologie Expérimentale et Comparée, Université Paris 13, Sorbonne Paris Cité, France.

Karen L. Hollis, Interdisciplinary Program in Neuroscience and Behavior, Mount Holyoke College, South Hadley, MA, USA, and Laboratoire d’Éthologie Expérimentale et Comparée, Université Paris 13, Sorbonne Paris Cité, France. Email: khollis@mtholyoke.edu (Corresponding author).

Abstract: Altruistic behavior, in which one individual provides aid to another at some cost to itself, is well documented. However, some species engage in a form of altruism, called rescue, that places the altruist in immediate danger. Here we investigate one such example, namely rescuing victims captured by predators. In a field experiment with two North American ant species, Tetramorium sp. E and Prenolepis imparis, individuals were held in artificial snares simulating capture. T. sp. E, but not P. imparis, exhibited digging, pulling, and snare biting, the latter precisely targeted to the object binding the victim. These results are the first to document precision rescue in a North American ant species; moreover, unlike rescue in other ants, T. sp. E rescues conspecifics from different colonies, mirroring their atypical social behavior, namely the lack of aggression between non-nestmate (heterocolonial) conspecifics. In a second, observational study designed to demonstrate rescue from an actual predator, T. sp. E victims were dropped into an antlion’s pit and the behavior of a single rescuer was observed. Results showed that T. sp. E not only attempted to release the victim, but also risked attacking the predator, suggesting that precision rescue may play an important role in this species’ antipredator behavior.

Keywords: rescue behavior, altruistic behavior, social insects, ants, Tetramorium sp. E, unicolonial social structure
Introduction

Rescue behavior provides aid appropriate to the distress of another, sometimes related, animal at a great cost to the rescuer and without immediate reward to the acting individual (Nowbahari and Hollis, 2010). Examples of rescue behavior in non-human animals include a male capuchin monkey helping a mother-infant pair flee a group of attackers (Vogel and Fuentes-Jiménez, 2006) and dolphins lifting an injured pod member to the surface to breathe instead of fleeing the fishing boat that caused the injury (Siebenaler and Caldwell, 1956). The species in both cases are mammals and, although these observational reports have gained attention, there is only one, very recent experimental study of rescue behavior in mammals (Bartal, Decety, and Mason, 2011). In contrast, rescue behavior – at least very simple forms of it – have been observed in ants as early as Belt’s 1984 monograph, and several more recent studies have revealed not only that ant rescue is much more complex than previously believed (Nowbahari, Scohier, Durand, and Hollis, 2009; Nowbahari, Hollis, and Durand, 2012), but also that rescuers are willing to face extreme risks (Czechowski, Godzińska, and Kozłowski, 2002).

The very structure of eusocial ants’ society is based upon an altruistic worker caste caring for offspring not their own (Bourke and Franks, 1995). Additionally, worker ants provide help for individuals in distress; for example, when one ant is trapped by dirt, nestmates have been observed digging the dirt away from the trapped ant, which generally results in the trapped individual being freed (Lafleur, 1940; Markl, 1965). More recently, ants have been observed engaging in what might be altruistic behavior that puts the altruist’s own safety in danger. For example, when driver ants, Dorylus spp., attack Pachycondyla analis soldier ants, small P. analis worker ants, the victims in these encounters, will attack the Dorylus ants clinging to the body of their soldier nestmates (Beck and Kunz, 2007). Indeed, P. analis worker ants that appeared to be fleeing the scene were observed turning back to join the fight, effectively aiding a struggling nestmate. Although the worker ants’ response may at first seem an obvious example of altruistic rescue, as the workers’ behavior alleviates the distress of a nestmate and places the rescuers in danger, the behavior may in fact have been self-defense, as suggested by the authors themselves.

Nonetheless, recent experimental studies provide clear evidence for actual rescue behavior in ants. In separate experiments, one conducted in the laboratory (Nowbahari et al., 2009) and another in the field (Hollis and Nowbahari, 2013), the ability to rescue was explored in six different species of sand-digging Mediterranean ants. In both studies, individual ants were tied to a piece of filter paper with nylon thread and partially buried in sand. In the presence of the entrapped victim, rescuers of three species, namely Cataglyphis cursor, Cataglyphis floricola, and Lasius grandis, not only engaged in the simple digging and pulling behaviors, but also exhibited two previously unknown rescue behaviors. That is, following their ineffective behavior to free the victim, rescuers then began to move sand away from the victim, exposing the nylon snare, and then targeted the snare with precise bites. Labeled precision rescue behavior by the authors, snare biting was carefully aimed, even though it was in direct contact with the victim’s body, thus suggesting that ants somehow were able to recognize what, exactly, held the victim in place.
Yet another report of ant rescue provides additional evidence that several ant species engage in behavior that meets the.Nowbahari and Hollis (2010) definition of rescue. When either *Formica sanguinea* or *Formica cinerea* workers were captured by predatory larval ant lions, nearby nestmates attacked the ant lion, dug in the dirt to uncover nestmates, and pulled on the limbs of the captured ant (Czechowski et al., 2002). Although the two forms of precision rescue behavior described by Nowbahari et al. (2009) were not reported in this study, it is possible that the authors simply failed to include them.

Because of their sedentary habits, pit-digging ant lions, such as those observed by Czechowski et al. (2002), provide a unique opportunity for studying rescue behavior under both field and laboratory conditions. Many ant lion species, members of the family *Myrmeleontidae*, build cone-shaped pits in loose, sandy soils during their larval stage. Pit traps not only allow for prey capture over a large distance, but also they inhibit prey escape and serve as a source of protection for the ant lion (Guillette, Hollis, and Markarian, 2009; Lucas, 1986). After an arthropod crawls past the edge of the trap and begins to lose its footing on the collapsing pit walls, it may spend time struggling to escape before it falls to the bottom of the pit where the ant lion waits with open mandibles. Once captured, the prey may struggle for a period of time before the ant lion is able to subdue it, often by flicking it back and forth against the pit walls (Griffiths, 1980). This somewhat long process makes successful rescue attempts possible. Indeed, we have observed ants alive and fully mobile after being held by an ant lion for over 10 minutes, all the more surprising because ant lions kill their prey by injecting poison through the mandibles (Griffiths, 1980).

The present study attempted to explore precision rescue behavior, and its role as an antipredator strategy, in two species of North American ants, *Tetramorium* sp. E (Schlick-Steiner et al., 2006) and *Prenolepis imparis*. These species were selected for three reasons, all of which enabled us to expand our knowledge of precision rescue in ants. One, both species share the same general habitat as pit-digging ant lions and, thus, provide an opportunity to study species for which rescue might serve as an important antipredator strategy. Two, *T*. sp. E differs in an important way from the three Mediterranean “rescuer” species studied by Nowbahari et al. (2009; 2012) and Hollis and Nowbahari (2013). Whereas all three of those species rescued only nestmates, displaying aggression toward ants of either another species or another colony, *T*. sp. E does not display aggression between non-nestmate conspecifics, suggesting – albeit on the basis of behavioral evidence only – that they may have a unicolonial structure (Steiner, Schlick-Steiner, and Buschinger, 2003). Unicolonial ants build extensive colonies that can include hundreds of nests between which workers and queens can move freely without aggression (Helanterä, Strassmann, Carrillo, and Queller, 2009). But whether or not *T*. sp. E is a unicolonial species, the lack of aggression between non-nestmate conspecifics gave us good reason to predict that, if *T*. sp. E were capable of engaging in rescue behavior, it would likely rescue all conspecifics, whether nestmates or not. Finally, three, although *Prenolepis imparis*, the other ant species chosen for this study, are of the same relatively small size as *T*. sp. E (0.3 cm) and, thus, would likely have difficulty escaping ant lions’ pits, they are not found in as close proximity to predatory ant lions as are *T*. sp. E ants. However, unlike *T*. sp. E, *P*. imparis exhibits no evidence of a unicolonial social structure and is highly aggressive toward ants of other species - often one of the dominant species in an ant community hierarchy (Fellers, 1989).
Thus, if *P. imparis* did engage in rescue behavior, it would be more likely to share the “rescue profile” of the three previously studied Mediterranean species, rescuing only nestmates.

**Experiment 1**

Experiment 1, a field study, compared the behavioral reactions to an artificially restrained ant, the victim, in two North American ant species, *Tetramorium* sp. E and *Prenolepis imparis*.

**Materials and Methods**

Tests were carried out in South Hadley, Massachusetts between May and July 2011. Each of four *T.* sp. E colonies and three *P. imparis* colonies, at least 150 ft. apart from each other, were tested under five different conditions: homocolonial tests, in which the live victim was a conspecific from the same test colony; heterocolonial tests, in which the live victim was a conspecific from a different colony; heterospecific tests, in which the live victim was a member of a different species; anesthetized nestmate tests, in which the victim was a nestmate that had been anesthetized by freezing, making it incapable of signaling alarm; and, control tests in which the paper-and-thread snare was empty. Only colonies that exhibited high activity levels and a large number of foragers present on the surface near the nest entrance were chosen for study. All data were collected during ants’ active period.

Filter paper snares were prepared in advance of all tests: Using a sewing needle, a small loop of two-ply cotton thread was inserted into a 1.0 x 0.5 cm piece of 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 container to avoid contamination; a new snare was used for each test.

**Procedure**

The testing procedures were similar to Hollis and Nowbahari (2013). Victim ants were captured after they were observed leaving the nest entrance of the colony and gently inserted into the thread loop, which then was tightened around the ant’s thorax. To insure that foragers would be likely to encounter the test stimulus, the snared ant was placed within 5 cm of the nest entrance and the paper was lightly covered with substrate from the nest area. Each test commenced within 10 seconds of positioning the snared ant, and was 5 minutes in duration.

For anesthetized nestmate tests, victims were placed in a small plastic container and refrigerated for a period of 15 minutes. After anesthetization the ant was snared as described above. Control tests were conducted using an empty snare not containing an ant, but in all other ways prepared as described above. Half of the heterospecific tests were conducted with a member of the other species being studied and half with *Formica* ants from a nearby colony.

**Data collection and analysis**

Six trials of each test type were obtained from each of the seven ant colonies (four...
T. sp. E and three P. imparis). All tests were recorded using Panasonic Mini DV Digital Camcorders, and data were collected during playback of the video-recorded trials. An interval recording procedure was used to collect all data: Each 5-minute trial was divided into 10-second intervals and target behaviors were recorded by interval. For each target behavior (see Table 1), the data were the proportion of intervals in which that behavior pattern was observed.

Each of the behavior patterns was subjected to a univariate analysis of variance (ANOVA) with two between-subjects factors, namely species and test type. In addition, because the individual rescue behavior patterns cannot capture the overall level of rescue, we also computed a “combined” rescue score.

Table 1. Operational definitions of target behavior patterns

| Behavior       | Operational Definition                                                                                                                                 |
|----------------|------------------------------------------------------------------------------------------------------------------------------------------------------|
| Sand digging   | Ant positions itself within 2 cm of, and facing, the test stimulus, either the ensnared ant victim or the paper-and-snare control stimulus, and flicks sand backward, away from the test stimulus, using its anterior legs (Experiment 1 only). The antennae are facing forward, in the characteristic non-aggressive posture. |
| Limb pulling   | Ant grabs limb of the ant victim with mandibles and drags it backwards with frequent antennation. The antennae are facing forward, in the characteristic non-aggressive posture |
| Snare biting   | Ant bites and tugs at the thread snare using mandibles (Experiment 1 only). The antennae are facing forward, in the characteristic non-aggressive posture. |
| Sand transport | Ant picks up, using its mandibles, one or more particles of sand/substrate covering the filter paper or ensnared ant victim (Experiment 1), or covering the victim while in the antlion pit (Experiment 2), and moves it at least one body length from its original position. The antennae are facing forward, in the characteristic non-aggressive posture. |
| Attack         | Ant engages in either of two aggressive behaviors (Experiment 2 only): Biting/dismembering, closing its mandibles around part of the antlion’s body, sometimes while also moving away from the antlion; or, stinging, directing its stinger toward the antlion, often while the gaster (abdomen) is flexed, curved underneath the body. All attack components are performed with the antennae flexed backward, in the characteristic aggressive posture. |

Results and Discussion

Although both species engaged in frequent approach to the test stimulus, which we insured by placing the victim close to the nest entrance, T. sp. E and P. imparis differed significantly in their combined rescue response to the test stimuli (see Figure 1). An
ANOVA revealed significant main effects of species, $F(1, 200) = 8.775, p = .003$, indicating that $T$. sp. E and $P$. imparis responded differently to the experimental conditions overall, as well as test type, $F(4, 200) = 3.468, p = .009$, indicating that the ant’s response varied between the test stimuli. Exploration of the significant interaction between species and test type, $F(4, 200) = 3.364, p = .011$, using Tukey’s post hoc tests revealed that, very much unlike $P$. imparis, $T$. sp. E engaged in rescue behavior on both homocolonial and heterocolonial tests, and performed significantly more rescue behavior during homocolonial tests than either heterospecific, anesthetized nestmate, and empty snare tests ($p = .003$, $p = .004$, and $p = .004$, respectively). However, in keeping with our predictions, $T$. sp. E provided rescue equally to both homocolonial and heterocolonial ants of the same species ($p = .999$), engaging in rescue behavior in 38% of homocolonial and 42% of heterocolonial trials. These findings are very much unlike previous results with the three Mediterranean rescuer species (Hollis and Nowbahari, 2013; Nowbahari et al., 2009), but consistent with observations that $T$. sp. E ants do not display aggression toward non-nestmate conspecifics and, possibly, have a unicolonial social structure (Steiner et al., 2003). Conversely, $P$. imparis performed rescue behavior in only one test, a heterocolonial test, which also included aggressive behaviors directed towards the snared conspecific. Both $T$. sp. E and $P$. imparis refused aid to all heterospecific victims, and also did not respond with rescue behavior during any of the control tests, either with an anesthetized nestmate or with an empty snare.

**Figure 1.** The mean proportion of intervals in which at least one individual engaged in some form of rescue behavior (i.e., combined score), in response to five kinds of test stimuli.

![Rescue Behavior – Combined Score](image)

**Notes:** Tests were conducted with each of two species, *Tetramorium* sp. E and *Prenolepis imparis*. Error bars reflect ± standard error of the mean.
As can be seen in Figure 2, which illustrates the types of rescue behavior performed in response to homocolonial victims, *T.* sp. E engaged in both sand transport and snare biting, the kinds of precision rescue behaviors first reported in *C. cursor* (Nowbahari et al., 2009) and more recently in *C. floricola* and *L. grandis* (Hollis and Nowbahari, 2013).

**Figure 2.** The mean proportion of intervals in which ants engaged in each of the four rescue behavior patterns during homocolonial test trials

![Rescue Behavior – Homocolonial](image)

*Notes: Tests were conducted with each of two species, *Tetramorium* sp. E and *Prenolepis imparis*. Error bars reflect ± standard error of the mean.*

**Experiment 2**

Although we postulated that the rescue behavior delivered by *T.* sp. E to an artificially ensnared conspecific also would occur if a conspecific were captured by an antlion, this premise required further testing. Because Experiment 1 already had included control groups designed to show that rescue is elicited only in the presence of an actively responding conspecific victim, Experiment 2, a semi-naturalistic observational study performed in the laboratory, was designed merely to demonstrate that *T.* sp. E would indeed enter an antlion’s pit and attempt to rescue a nestmate captured by a live antlion.

**Materials and Methods**

The ant subjects were obtained from two wild *T.* sp. E colonies taken from the grounds of Mount Holyoke College, South Hadley, MA, and moved into the laboratory. Each colony was kept in a 10-gallon aquarium tank filled with commercially available...
garden soil. The upper walls of the aquarium were coated with fluon (“Insect-A-Slip”), which prevents ants from escaping. Ants were maintained on a mixture of honey water ad libitum, and fed mealworms two to three times each week. Colonies were misted with water daily to prevent dehydration.

Antlions were wild captured larvae (Myrmeleontidae sp.) obtained from AntLionFarms.com, Pensacola, Florida. After arrival, antlions were placed individually in small round plastic food bowls (4 x 15 cm diam), filled with fine sanitized Estes Marine Sand. A plastic ring (“pit ring”) was placed on top of the sand in the middle of each bowl, a technique for insuring that antlions dug pits in the center of each bowl. (Details of antlions’ housing and maintenance are described in Guillette et al., 2009). Antlions used in this study were selected based upon their weight and pit size: Only antlions that weighed between 0.035 and 0.055 grams, and dug pits that were at least 3.0 cm deep and 3.5 cm wide were chosen. Pit rings were removed after pits were established.

Before each test, two ants were removed from the surface of one colony and placed in an empty plastic bowl, the walls of which were coated with fluon. One member of the pair, randomly chosen as the victim, was picked up and gently rolled between the experimenter’s fingers, and then dropped, still alive, directly into an antlion pit. This procedure stunned the ant and injured its legs, which prevented escape from the antlion. Sixty seconds after the victim was dropped and grabbed by the antlion, the remaining pair member was placed halfway between the edge of the bowl and the edge of the antlion pit. Once the potential rescuer entered the antlion pit, behavior was video recorded for 5 minutes, or until the potential rescuer climbed out of the pit. Both ants were left in the bowl for the antlion to consume. After antlions consumed the prey and threw both carcasses from its pit, the antlion was removed, the sand in its bowl was replaced by fresh sand, and the antlion was placed back into the bowl and given time to build a new pit. Antlions were used again after 3 days if they met the criteria for inclusion, described above. A total of 58 trials were conducted. Target behaviors, described in Table 1, were scored during video playback.

Results and Discussion

In 36% of trials, individual T. sp. E ants responded to a nestmate captured by an antlion and performed rescue behavior (see Figure 3). This percentage of rescue attempts, which is nearly the same as occurred in the homocolonial trials of Experiment 1 (38%), is surprising given that, in Experiment 2, only one potential rescuer was present. That is, previous research (Nowbahari et al., 2009, 2012) has shown that, often, at least several foragers must be present for rescue to be elicited, a condition that our field experiment essentially duplicated but which was not the case in Experiment 2. Nonetheless, and despite this potential limitation, in the present experiment T. sp. E rescuers pulled on the limbs of nestmates held by a live predatory antlion and transported sand away from covered nestmates. In addition, T. sp. E rescuers responded to the predator by attacking it. Antlion attacks took several forms: Rescuers bit the antlion, attempted to dismember it by pulling on its mandibles, and stung the antlion.
Figure 3. The mean proportion of intervals in which *Tetramorium* sp. E rescuers engaged in each of three rescue behavior patterns

| Behavior     | Mean Proportion |
|--------------|-----------------|
| Pulling      | 0.25            |
| Sand transport | 0.1            |
| Attack       | 0.05            |

*Note:* Error bars reflect ± standard error of the mean.

Although our experimental procedure of rolling the victim prior to placement in the pit not only prevented its escape, but also, more importantly, rendered it incapable of augmenting the efforts of the rescuer, four of the rescue attempts were successful in that the rescuer either pulled the victim out of the mandibles of the antlion or caused the antlion to open its mandibles and release the victim. In several cases the antlion responded to the rescuer by abandoning the prey and burrowing under the sand, one of several ways that antlions circumvent the antipredator tactics of their prey (Eisner, Baldwin, and Conner, 1993). Finally, in one trial, which clearly demonstrates the risk to rescuers’ own safety, the victim was released following a successful rescue attempt, whereupon the rescuer was grabbed by the antlion and the original victim, now freed, began to pull on the limbs of the captured rescuer.

The purpose of this observational study was simply to determine whether the rescue behavior patterns that occurred in Experiment 1 would be performed in an actual encounter with a live predator. Interestingly, in Experiment 2 we observed attacks on the antlion itself in almost exactly the same proportion of intervals that we had observed snare biting in Experiment 1 (cf. Figures 2 and 3). Clearly, however, limb pulling, behavior that would appear to be the safest tactic for the rescuer because it could remain at some distance from the predator, was the predominant behavior. Digging, which could have made the pit walls steeper and thus exacerbated the problem – but in any case would not likely have aided the victim – was never observed.

**General Discussion**

Taken together these experiments demonstrate that at least one North American ant species, *T*. sp. E, is capable of providing precision rescue behavior for nestmates,
expanding the work of Nowbahari et al. (2009) and Hollis and Nowbahari (2013) on several Mediterranean species. Moreover, T. sp. E not only rescued nestmates, but also extended that same aid to conspecifics from other colonies, a significant departure from rescue behavior in Mediterranean ants, but which is consistent with the hypothesis that it may have a unicolonial structure (Steiner et al., 2003). Finally, T. sp. E directly attacked predatory antlions, placing rescuers at very high risk of being captured themselves, as actually occurred in our observational study.

Whenever T. sp. E provided rescue to distressed conspecifics, the rescue attempts appeared to be precisely directed to the actual threat. That is, when a piece of thread was the restraining device, T. sp. E bit the thread, moved sand away from it, which exposed the thread further, and continued biting at the thread. When, however, an antlion’s mandibles restrained the victim, T. sp. E employed very different tactics, namely precisely directed dismembering and stinging behavior instead. Although precise rescue behavior in ants is certainly the result of relatively simple behavioral algorithms, the underlying mechanisms controlling this behavior would seem to be a bit more complex than what would be needed to elicit digging and pulling. For example, a call-for-help signal, such as an ant alarm pheromone (Blum and Warter, 1966; Hangartner, 1969; Spangler, 1968; Wilson, 1958) could be used to alert conspecifics, producing frenetic movement in multiple directions as the rescuer attempts to orient toward the source. After the rescuer detects the source, it then simply follows the signal’s sensory gradient until it makes contact with the victim. Then, once contact has been made, involving, for example, a cuticular hydrocarbon recognition mechanism in ants (Hölldobler and Wilson, 1990; Howard, 1993; Howard and Blomquist, 2005), the rescuer digs and pulls. It is difficult to see, however, how these kinds of simple releasing mechanisms could guide ant rescuers to the precise location of whatever object is holding the victim in place, enable them to transport sand away from this object, exposing it further, and then to target their bites and stings to the object itself, transporting additional sand as necessary. Additional research is required to explore what appear to be more complex mechanisms.

Although not all potential rescuers engaged in rescue behavior, it is likely either that some critical threshold was not reached, or that some individuals are less capable of rescuing than others, as has been demonstrated in C. cursor (Nowbahari et al., 2012). Similarly, in several species of social insects where extremely risky behaviors are a possible response to nest threats, some individuals perform self-preservation behaviors even when the nest is in direct danger (Shorter and Rueppell, 2012). Thus, our data, which revealed that not all individuals help a conspecific and that victims sometimes are ignored, do not detract from the finding that T. sp. E is capable of engaging in what appears to be an effective antipredator strategy.

Despite the fact that colonies of P. imparis were found in the same general habitat as antlion pits, albeit not in close proximity to them, and that its small size would render it easy prey for antlions, this species rarely if ever engaged in rescue of any kind; moreover, even on the one occasion in which P. imparis ants did respond to a nestmate, they never exhibited snare biting or sand transport. These differences between species suggest that rescue behavior – or, at a very minimum, precision rescue behavior – is not necessarily a trait found in all ant species. Thus, other ecological factors, which this study was not
designed to elucidate, must be influencing this behavior (but see Hollis and Nowbahari, 2013, for a discussion of ecological variables associated with rescue behavior). Nonetheless, our results provide evidence that there is variety in this trait, necessitating a broader comparative study of rescue behavior in multiple species from different families. Finally, attempts to measure the true frequency of successful rescue behavior in the wild would provide a deeper understanding, not only of the predator-prey relationship between ants and antlions (Hollis, Cogswell, Snyder, Guillette, and Nowbahari, 2011; Hollis and Guillette, 2011; Lucas and Brockmann, 1981), but also of this extreme form of altruism—a behavior that appears to have evolved in many animals.

Acknowledgements: This research was supported by a Faculty Grant from Mount Holyoke College (KLH) and by funding from Mount Holyoke’s Ellen P. Reese Fund (KT and AV). The Laboratoire d’Éthologie Expérimentale et Comparée, Université Paris 13 provided additional support (EN and KLH).

Received 28 August 2011; Revision submitted 05 November 2012; Accepted 09 November 2012

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