

## Original Article

### Toward a Behavioral Ecology of Rescue Behavior

Karen L. Hollis, Interdisciplinary Program in Neuroscience and Behavior, Mount Holyoke College, South Hadley, MA, USA. Email: [khollis@mtholyoke.edu](mailto:khollis@mtholyoke.edu) (Corresponding author).

Elise Nowbahari, Laboratoire d'Éthologie Expérimentale et Comparée (EA 4443), Université Paris 13, Sorbonne Paris Cité, F-93430 Villetaneuse, France.

**Abstract:** Although the study of helping behavior has revolutionized the field of behavioral ecology, scientific examination of rescue behavior remains extremely rare, except perhaps in ants, having been described as early as 1874. Nonetheless, recent work in our laboratories has revealed several new patterns of rescue behavior that appear to be much more complex than previously studied forms. This precisely-directed rescue behavior bears a remarkable resemblance to what has been labeled empathy in rats, and thus raises numerous philosophical and theoretical questions: How should rescue behavior (or empathy) be defined? What distinguishes rescue from other forms of altruism? In what ways is rescue behavior in ants different from, and similar to, rescue in other non-human animals? What selection pressures dictate its appearance? In this paper, we review our own experimental studies of rescue in both laboratory and field, which, taken together, begin to reveal some of the behavioral ecological conditions that likely have given rise to rescue behavior in ants. Against this background, we also address important theoretical questions involving rescue, including those outlined above. In this way, we hope not only to encourage further experimental analysis of rescue behavior, but also to highlight important similarities and differences in very distant taxa.

**Keywords:** rescue behavior, altruism, helping behavior, eusocial insects, ants, empathy, division of labor

---

### Introduction

From ants to elephants, helping behavior is ubiquitous throughout the animal kingdom (Dugatkin, 1997; Lehmann and Keller, 2006). Although helping and other forms of altruistic behavior often were described as being “for the good of the species” in the 1950s and 1960s, the seminal ideas of kin selection and reciprocal altruism (Dawkins, 1976, 1982; Hamilton, 1963, 1964; Trivers, 1971) replaced such group selection arguments

with powerful explanatory principles that not only changed the way scientists approached altruistic behavior, but also spurred the search for new examples. No doubt the ubiquity of helping behavior in contemporary scientific literature is the result of that intense search for new forms of helping—in new environments and in new species. Metaphorically speaking, scientists were outfitted with a “search image” for helping behavior, and thus discovered it in previously overlooked places. In this paper, we focus the scientific spotlight on rescue behavior, a form of helping behavior that has been observed in only a few, distant taxa, and in this way encourage further experimental analysis. In addition, we hope to prompt further examination of cross-species similarities and differences in an attempt to explain this especially costly form of altruism at both proximate and ultimate levels.

Before we discuss rescue behavior, however, an important caveat is in order: We recognize that our use of the term “altruism” may be very different from its use in the anthropological, social psychological, and philosophical literatures. Here, we use it in the biological sense, meaning any behavior that increases the fitness of the receiver, and which carries some cost to the altruist. In this biological sense, however, altruistic acts are recognized as providing fitness benefits to the altruist. These benefits may come about either because, according to kin selection theory (Hamilton, 1963, 1964), altruistic acts increase the fitness of genetically related individuals, called *inclusive fitness*, or when altruistic acts are reciprocated at a later date, called *reciprocal altruism*, or sometimes more simply, *reciprocity* (Dugatkin, 1997; Lehmann and Keller, 2006; Trivers, 1971).

### **Observational Studies of Rescue Behavior**

Although many anecdotes of rescue can be found throughout the popular media, scientific reports of rescue in the wild, even rescue of a conspecific, are extremely rare. In the earliest, often-cited example of vertebrate rescue behavior, several dolphins assisted a pod member that had been injured in a fishing operation (Siebenaler and Caldwell, 1956). As described by the authors, an adult dolphin that had been stunned by exploding dynamite began racing around the area of the fishing vessel, exhibiting a 45° “list.” Almost immediately, two other adults, both members of the nearby pod, swam to the victim, placed their heads just under the injured animal’s pectoral fin, and lifted it to the surface “in an apparent effort to allow it to breathe while it remained partially stunned” (p. 126). The authors are careful to point out that all members of the pod remained nearby until the victim recovered, and then left at very high speed; a high-speed departure, the authors report, was the course of action after another, similar explosion when no individuals were hurt. In addition to the obvious risk of injury by subsequent explosions, those rescuers supporting the victim were forced to remain underwater, limiting their own ability to breathe. Although the rescuers were not at risk of drowning, their rescue behavior nonetheless involved both high risks and costs.

In another observational report of rescue behavior in the scientific literature (Vogel and Fuentes-Jiménez, 2006), a female capuchin monkey and her 10-day-old infant became isolated from their group in an intergroup encounter. Six male attackers had prevented the female and her infant from escaping with the others, and the males were attempting to grab the infant. Infanticide appeared imminent and the female responded with loud alarm calls.

Although the beta male from her own group initially had fled the encounter, he returned within minutes of the female's alarm calls and, even though alone in his efforts, he gave an intense threat vocalization, whereupon the attackers left the mother-infant pair and chased him instead. The female and her infant thus were able to rejoin their group immediately; the beta male rescuer, however, was not able to return until much later, presumably because he still was evading attack. What is especially interesting to us about this report, beyond the obvious risk to the rescuer, is that this first published evidence of rescue behavior in capuchin monkeys, coalition-forming animals that are well known for their extensive helping behavior, appeared only six years ago, despite decades of behavioral research by countless investigators. In short, naturally occurring rescue behavior may be difficult to observe because it is rare or, perhaps, because we are not prompted to search for its appearance. To help identify rescue behavior, we have developed a definition that distinguishes it from cooperation and other forms of altruistic behavior (Nowbahari and Hollis, 2010). In this way, we hope to stimulate research in this area, which, in turn, will lead to a more comprehensive understanding of the role that rescue plays in group-living species, as well as the selection pressures that have shaped the specific contexts in which it appears.

### **Toward a Definition of Rescue Behavior**

Identifying rescue behavior requires a “working definition.” To this end, Nowbahari and Hollis (2010) proposed four components, which we review below. In the present paper, we attempt to build upon these ideas, expanding our working definition in light of more recent work.

#### *Component 1: The victim is endangered*

Although we originally proposed (Nowbahari and Hollis, 2010) that the victim must be “in distress,” namely in a situation that poses an immediate physical risk to itself, we did not intend to suggest that the victim necessarily must be conscious or somehow aware of its dangerous situation. Thus, “endangered” is, perhaps, a better descriptor to drive home the critical point that the victim will suffer severe physical harm if it is not rescued or does not escape the current situation. This restriction to situations involving severe physical harm helps to differentiate rescue behavior from situations involving other, less extreme fitness costs suffered by the individual being helped. For example, female Rodrigues fruit bats assist pregnant conspecifics in the birthing process (Kunz, Allgaier, Seyjagat, and Caliguirri, 1994), a form of cooperative behavior that likely results in easier deliveries; however, under normal circumstances, the mother is not in danger of severe physical harm. Likewise, a cheetah parent is not said to rescue its cub if it delivers food when the cub is hungry or if it prevents its offspring from engaging in behavior that is merely energetically costly, as when the parent helps to improve the cub's predatory abilities (Caro, 1994). Although short-term metabolic costs certainly represent reductions to fitness—and although an endangered victim may indeed accrue such costs if it attempts to escape the distressful situation—short-term metabolic costs and other forms of fitness costs are, in themselves, neither necessary nor sufficient to define endangerment. If, however, the cub is about to

wander too close to a predatory snake, parental intervention would constitute rescue behavior.

At first glance, our insistence that the victim risks severe physical harm might appear too limiting. However, the physical consequences of the distressful situation need not always be direct, as when, for example, a stunned dolphin is at risk of drowning or a capuchin infant would surely be killed if grabbed by its attackers. Instead, the physical consequences could be indirect, resulting from chronic stress. For example, humans are said to rescue women and children from emotionally abusive domestic situations when they provide alternative places to live. Chronic stress does not produce immediate physical harm; nonetheless, it elicits a cascade of deleterious physical and genetic changes via the endocrine system that does, indeed, result in severe physical harm (e.g., McEwen and Seeman, 1999; Sapolsky, 1996).

Although many examples of rescue behavior might involve a call-for-help, which is released by the victim and detected by potential rescuers, we do not propose that a definition of rescue behavior necessarily must include such communication, even if it appears to be necessary in some animals (Hollis and Nowbahari, 2013; Nowbahari, Scohier, Durand, and Hollis, 2009; see also Taylor, Visvader, Nowbahari, and Hollis, this issue). Rescue attempts by humans may be made in the absence of such calls, which leaves open the possibility that the same is true in other non-human animals. Thus, although a call-for-help may be necessary to elicit rescue behavior in some species—indeed, it may constitute the means whereby individuals recognize that another individual is endangered—the eliciting stimulus does not need to be part of the definition of rescue behavior.

*Component 2: The rescuer places itself at risk of endangerment by engaging in a rescue attempt*

This component of rescue behavior marks it as a special case of helping, an act that might be called extreme altruism, because of the especially large risks involved. In limiting rescue behavior in this way, we intend to reserve it for a special place along a continuum of increasingly costly altruistic behavior.

Nonetheless, we recognize that no hard-and-fast line always will separate rescue from other forms of helping, even if rescue does represent one end of a cost continuum. A case in point is the food-sharing that occurs between female vampire bats (Wilkinson, 1984, 1990). Because vampire bats need frequent blood meals to survive, an individual that has failed to obtain food is in very real danger of starvation. Food sharing in the form of a regurgitated blood meal often occurs between hungry and satiated females, and Wilkinson (1984, 1990) was able to show that both kin selection and reciprocity were at work. However, what makes this case unclear vis-à-vis our definition of rescue is that, although the hungry individual is very much in severe physical distress, it is not yet clear whether the cost to the female providing the regurgitated meal places her, the altruist, at great risk. Similarly, human parents—and even bystanders—whisk children away from dangerous ledges and windowsills, or grab them if they accidentally wander too close to the edge of subway platforms. However, even though the sight of the child in danger is momentarily stressful to the adults involved, unless those adults themselves are endangered, we propose not to call this behavior rescue. To us, there seems to be something profoundly,

qualitatively different between the relatively commonplace act of reaching out to grab a child in danger, and such feats as throwing one's body over a child caught between the tracks, protecting the child while the train passes overhead. Of course, the risk to the rescuer need not always be so extreme. Nonetheless, we propose to define rescue narrowly; true rescue behavior must endanger the rescuer, at least to some extent.

*Component 3: The behavior of the rescuer is generally suited to the circumstances of the victim's distress or endangerment*

Not all rescue attempts are successful. Thus, rescue behavior must be defined without reference to its outcome. In addition, if the definition is to be generalizable and thus applied to such distant taxa as ants, monkeys, dolphins, and humans, then it must avoid reference to "intentionality" on the part of the rescuer, a point to which we return later in this paper. For example, pulling on the limbs of a trapped nestmate does not require that an ant "intends" to release the victim, nor does it require that the ant "recognizes" either the distress of the victim or the potential outcome of its actions. Nonetheless, in an attempt to capture the essence of rescue behavior while, at the same time, to avoid instances in which the victim serves as a releaser for behavior that is completely unrelated to its distress, we propose that the behavior of the rescuer be somehow relevant to the distressful event. For example, a victimized adult may be approached by its offspring begging for food or seeking contact. Of course, relevance may be in the eyes of the beholder, and all cases may not be so unambiguous. Although we recognize the ambiguity of this definitional component, it allows us to exclude irrelevant acts, like food begging, without necessitating that rescue behavior always be either efficient or successful.

*Component 4: The act of rescuing is not inherently rewarding or beneficial to the rescuer*

We argue that, for a behavior to be labeled rescue, it must carry no reward or benefit, except, of course, the fitness benefit that accrues from kin selection or reciprocal altruism—the *raison d'être* of all altruistic behavior, including rescue. This component helps to distinguish rescue behavior from various forms of cooperation, for example *byproduct mutualism* (Connor, 1995), in which individuals engage concurrently in behavior that benefits all parties simultaneously.

An example of this form of cooperation, which underscores the importance of a rigorous definition of rescue behavior, is a case reported by Beck and Kunz (2007), which they label—rightly so in our opinion—"cooperative self-defense" among ants. They show that, when attacked by driver ants, victimized *Pachycondyla analis* ants engage in counterattack behavior; in addition, however, they report that *P. analis* victims sometimes turned back to attack a driver ant that was injuring a conspecific, an act that would seem to qualify as rescue behavior. However, it is impossible in this case to distinguish between rescue behavior and self-defense: Did the individual interrupt its own escape and turn back to rescue its nestmate, or did the counterattack just happen to be elicited as the individual was in the process of moving away? We argue that the behavior should not be described as a definitive case of rescue, at least not yet, which is likely the reason the authors themselves use the term "cooperative self-defense" in the title of their paper instead of "rescue."

This restriction would seem to pose a problem if one wishes to include human

behavior. That is, heroic acts of rescue often are rewarded with medals, commendations, and all varieties of laudatory fanfare that befit heroic acts. However, one needs to distinguish between the reward inherent to the situation and the reward that may, or may not, be given if the act is recognized. In the same way that Caro and Hauser (1992) define teaching in animals as having no inherent reward—even if many of us human animals are rewarded in some way for “good teaching”—we, too, want to make the distinction between inherent rewards and benefits that derive directly from performing a behavior and those that may or may not be provided. In the case of rescue behavior in humans, rewarding highly visible examples of rescue behavior certainly encourages heroism in the culture, a case of a culturally “extended phenotype” (Dawkins, 1976). However, there are many unsung heroes in our midst: Most instances of rescue behavior, like good teaching, go unrewarded—and yet the behavior persists.

Each of these four components characterizes the observational studies of rescue behavior in dolphins (Siebenaler and Caldwell, 1956) and capuchin monkeys (Vogel and Fuentes-Jiménez, 2006) described earlier. In addition, however, our definition of rescue also captures perfectly the behavior of ants and rats, which have been subject to experimental analysis, and which we review next in an attempt to highlight what are several important commonalities across all species that exhibit rescue behavior.

### **Experimental Analysis of Rescue Behavior in Ants**

In ants, invertebrates well known for their highly integrated and complex cooperative behavior, anecdotes of a simple form of rescue behavior, namely sand digging, were described as early as 1874 (Belt, 1874). Subsequent reports of digging behavior, sometimes accompanied by limb pulling, appeared in the mid-1900s (Blum and Warter, 1966; Forrest, 1963; Hangartner, 1969; Lafleur, 1940; Markl, 1965; Spangler, 1968; Wilson, 1958). Recently, rescue behavior was reported in *Formica* ants trapped in the pits of predatory antlion larvae (Czechowski, Godzińska, and Kozłowski, 2002), common insect predators of many ant species (Guillette, Hollis, and Markarian, 2009; Hollis, Cogswell, Snyder, Guillette, and Nowbahari, 2011; Hollis and Guillette, 2011; see Figure 1). Czechowski and colleagues (2002) not only report extensive digging in *Formica* workers, but also limb-pulling behaviors.

In a laboratory experiment designed to simulate a natural situation in which another species of sand-dwelling ants, *Cataglyphis cursor*, become trapped, either by collapsing sand and debris, or by pit-digging antlions, Nowbahari et al. (2009) reported two additional, more complex forms of rescue behavior. In their experiment, victims were tied to a small piece of filter paper with nylon thread and placed in a small arena with a group of potential rescuers near the rescuers’ nest entrance. The victim was either (1) an individual from the same colony (homocolonial test); (2) an individual from a different colony of *Cataglyphis cursor* (heterocolonial test); (3) an ant from a different ant species (heterospecific test); (4) a common prey item; or, (5) a nestmate anesthetized by chilling (control test). In the final condition, an additional control test, the test stimulus consisted of (6) the empty snare apparatus.



**Figure 1.** A larval pit-digging antlion (*Myrmeleon* sp.) exposed on the sand surface (top left), and in the process of burying itself under the sand (top right). Bottom: Funnel-shaped antlion pits in fine sand

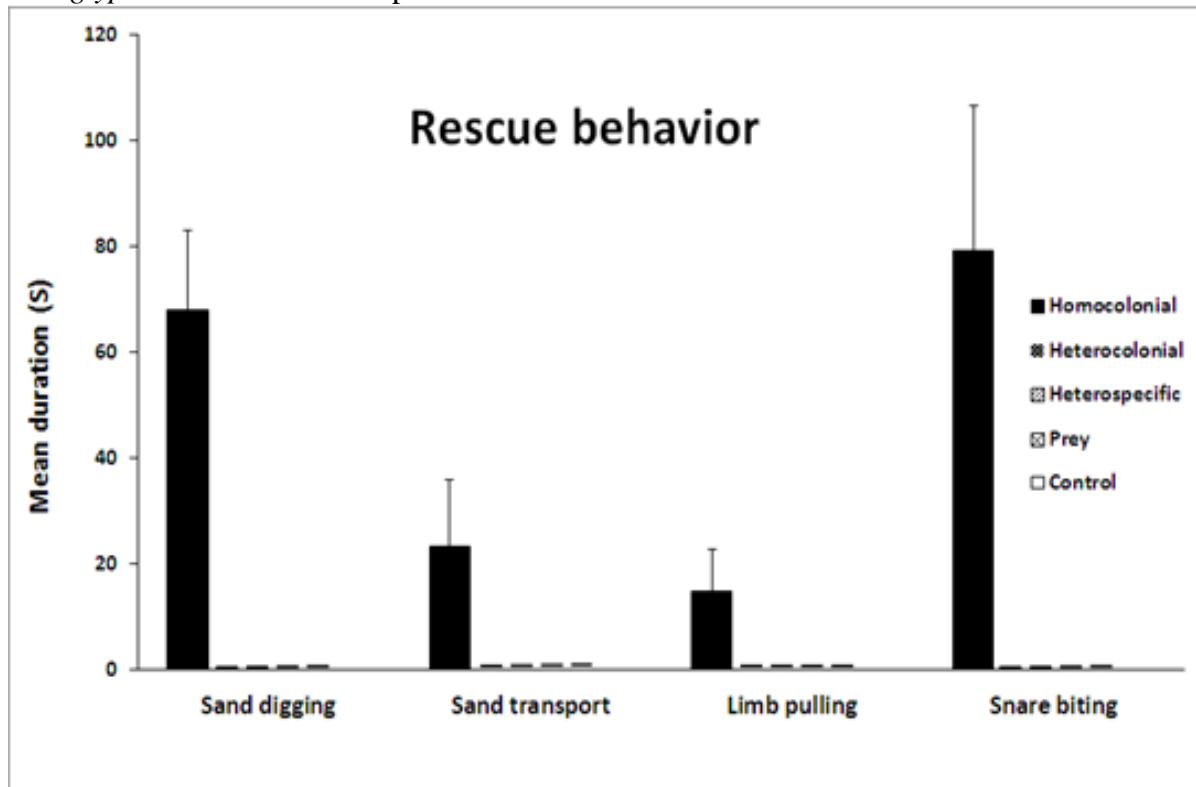


*Notes:* The winding furrows on the right side of the bottom photograph are the characteristic tracks made by antlions as they search for a suitable pit location. Photography by Cheryl McGraw. Adapted from Hollis et al., 2011.

The results of this experiment reveal that only active nestmates (i.e., homocolonial tests) evoked any form of rescue behavior. Rescue behavior never was observed in any of the remaining tests, either with live test individuals—i.e., heterocolonial ants, heterospecific ants, prey stimuli, and ensnared motionless (anesthetized) nestmates—or with an empty snare apparatus. As Figure 2 illustrates, rescue attempts consisted of digging sand in the area of the ensnared nestmate, transporting particles of sand away from the snare, sometimes as far as 2 cm, pulling the limbs of the ensnared nestmate (but never the antennae, highly sensitive appendages that could be injured easily) and, most important,

biting precisely at the nylon snare that entrapped the nestmate. In all of the homocolonial tests, rescuers began by digging and, often, transporting sand away from the victim before they attempted to extricate the victim by limb pulling, which exposed the snare. Rescuers then were able to direct their behavior toward the snare itself, digging and transporting additional sand, as needed, to expose more of the snare, to which they returned again and again. Figure 3 shows a close-up of snare biting by a *C. cursor* ant.

**Figure 2.** Mean duration of four rescue behavior patterns performed by groups of 5 *Cataglyphis cursor* ants in response to an ensnared test stimulus



Notes: Error bars reflect  $\pm 1$  standard error. Adapted from Nowbahari et al., 2009.

Subsequent work has revealed that other ant species are capable of what we call “precision rescue,” a combination of behavior patterns that includes snare biting and sand transport. In a field study of five Mediterranean ant species (Hollis and Nowbahari, 2013), two additional species engaged in vigorous rescue behavior, namely *C. floricola* and *Lasius grandis*. We argue that the behavioral ecology of these species is consistent with this difference in rescue behavior. That is, *C. floricola* and *Lasius grandis*, the rescuer species, belong to the same subfamily, Formicinae; both are located in fine, easily disturbed soils; both species locate their nests in areas frequented by large marauding ungulates and thus risk nest collapse; both species are prey of nearby antlions; and both species forage individually. The non-rescuer species, on the other hand, belong to the subfamily, Myrmicinae, and inhabit hard, compact soils. Moreover, two of the non-rescuer species, *Messor maroccanus* and *Messor barbarus*, form ant trails to food and thus are in very close



proximity to other individuals which they could grab, if needed, in what we hypothesized could be a form of “self-rescue.” Our work on rescue in ants also has extended to a North American species, *Tetramorium* sp. E (formerly *T. caespitum*), the common pavement ant (Taylor, Visvader, Nowbahari, and Hollis, this issue), which reveals that it too is capable of precision rescue, but in a very interesting way that distinguishes it from the Mediterranean species that we have studied thus far. In short, *T.* sp. E ants form very large colonies with multiple nests between which individuals move frequently, a feature that may explain why these ants—unlike all others that we have studied thus far—also rescue individuals from other nests.

**Figure 3.** In this photograph, a *C. cursor* rescuer already has transported sufficient sand away from the victim, exposing the nylon thread snare holding its nestmate in place (part of the white filter paper has been exposed as well), and is shown biting the nylon thread snare that holds the victim to the paper

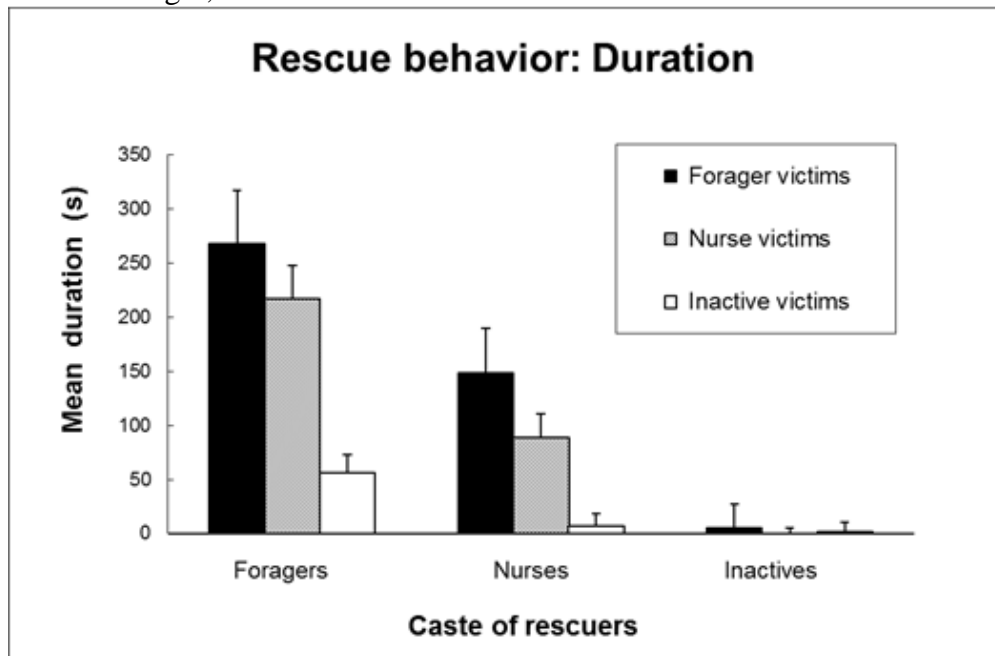


*Notes:* Individuals were marked for identification purposes. Photograph by Paul Devienne. Adapted from Nowbahari et al., 2009.

Finally, closer inspection of rescue in *C. cursor* (Nowbahari, Hollis, and Durand, 2012) has revealed that its rescue behavior is controlled by a division of labor, a form of *temporal polyethism* in which individuals specialize in performing different tasks—including foraging, defense and brood care—as they mature: As Figure 4 shows, foragers, the oldest individuals and the only adults to leave the nest, were able to administer and obtain the most help, while members of the youngest, inactive caste not only failed to respond to victims but also received virtually no help from potential rescuers, regardless of caste. Nurses performed intermediate levels of aid, mirroring their intermediate caste status. We argue that this division of labor in the ability to rescue a nestmate is a highly adaptive

specialization that is finely tuned to a caste member's probability of becoming, or encountering, a victim in need of rescue. That is, because *C. cursor* foragers, as in all ant species, are the only colony members to journey far from the nest, they are the only individuals that might become trapped as they travel in search of food, whereas nest-bound inactives would be less likely not only to require rescue, but also to provide aid to distant foragers. Finally, nurses, specialized for brood care, might require some of the same behavioral patterns needed by efficient rescuers.

**Figure 4.** Mean duration of rescue behavior performed by *C. cursor* rescuers, either all foragers, all nurses, or all inactives, in the presence of a single experimentally ensnared victim, either a forager, a nurse or an inactive



In sum, although a much more thorough comparative analysis of ant species is required, our findings begin to suggest that both cooperative living—especially in groups where individuals may be closely related—and risk of entrapment are key to rescue behavior. A recent study of rats, reviewed next, not only adds more detail to this emerging picture of rescue behavior, but also demonstrates the need for caution when interpreting the behavior of non-human animals.

### Experimental Analysis of Rescue Behavior in Rats

In an experiment similar to our work with ants, Bartal, Decety, and Mason (2011) studied the ability of rats to come to the aid of a distressed cagemate. After being housed together for 2 weeks, one member of each rat pair was restrained in a narrow acrylic tube placed in the center of an open arena; its cagemate, the “free rat,” was released into the same arena. Each pair was tested once per day for 12 days. An added dimension of the rat study, however, was that the free rat could liberate the victim by tipping open a door on the

Evolutionary Psychology – ISSN 1474-7049 – Volume 11(3). 2013. -656-

end of the restraining tube, an instrumental behavior aided by the experimenter who opened it half-way if the free rat failed to do so. Controls for this experiment included an empty restrainer, a restrainer with a toy rat inside, and an empty restrainer with the supposed “victim” placed, instead, on the other side of a perforated partition but otherwise completely free to move about.

The results of this rat experiment are remarkably similar to our own work with ants: Rats held in the restrainer produced a call-for-help, in this case ultrasonic vocalizations; also like ants, free rats became frenetic at first, circling the restrainer, and then began to bite and dig at the restrainer; finally, again like ants, rats attempted to pull the victim out of its restraint. In the case of rats, however, pulling was directed at the victim’s tail, the only body part available. Eventually, however, free rats learned to open the door, albeit with the experimenter’s help. Interestingly, so did some of the ants in our comparative field study (Hollis and Nowbahari, 2013); that is, despite our best efforts to tie ant victims securely, on a few occasions, ants were able to bite through the thread and release the victim.

Departing from our research with ants, however, a dependent variable in the Bartal et al. experiment (2011) was the amount of time the free rats spent in the center of the arena near the restrainer, which increased over days only in the rescue condition. In addition, more door openings occurred in the rescue condition than in the control conditions, although rats did occasionally open the door in the control conditions, unlike the behavior of ants, which never bit at the thread snare in any of our control conditions.

In the words of the authors, their study was designed “to determine whether rats are capable of empathically motivated helping behavior” (Bartal et al., 2011, p. 1427). Based on these results, together with two additional studies showing that (a) rats, having previously learned to open the door, would continue to do so even without direct contact with the released victim and, (b) rats would open a second restrainer to obtain chocolate and share it with a released victim, the authors argue that rats “acted intentionally to liberate a trapped conspecific” (Bartal et al., 2011, p. 1430). The most parsimonious explanation of their results, they argue further, is that rats possess “the ability to understand and actively respond to the [conspecific’s] affective state” (Bartal et al., 2011, p. 1430).

In a response to these claims, entitled “Pro-sociality without empathy,” Vasconcelos, Hollis, Nowbahari, and Kacelnik (2012) argued that the authors’ use of the terms “intended” and “empathically motivated” need clarification, and further, that claims of empathically motivated behavior require several extra steps that unfortunately were missing from the study of rat behavior. Here we will review the arguments made by Vasconcelos et al. (2012) in an attempt to show how these particular problems go far beyond the single paper on rat empathy, and in fact touch on many important theoretical questions involving rescue behavior.

First, Bartal et al. (2011) define pro-social behavior as “actions that are intended to benefit another” (p. 1427). If the word “intended” is simply a communicatory shortcut, meaning “designed by natural selection to benefit another,” then, as Vasconcelos et al. (2012) argue, the word merely stands for a functional explanation. This kind of communicatory shortcut is similar to biologists’ use of terms like “deception.” For example, Darwin’s monograph, “On the various contrivances by which orchids are fertilised by insects” (1877), is replete with examples of the ways in which orchid flowers

“deceive” insects into pollinating them. Deception through mimicry of this sort takes countless other forms as well; another recent example of deception is found in male swordtail characin fish, which lure females into an especially efficient mating posture by dangling a body part that functions as an ant-like food lure (Kolm, Amcoff, Mann, and Arnqvist, 2012).

Vasconcelos et al. (2012) argue that this functional use of the word intended is perfectly acceptable. However, we suggest that, because its use is ambiguous, it is very misleading and thus should be avoided. If, on the other hand, “intended to benefit another” is used to mean that rats were psychologically motivated to improve their cagemates’ wellbeing, then, as Vasconcelos and co-workers assert, the experiments with rats miss the mark entirely. What are sorely needed are control groups that help to show what, exactly, is driving the rats’ behavior: Is the motivation actually the wellbeing, or welfare, of another individual? Or does the motivation in fact derive from variables affecting only the rescuer, per se? Readers will recognize that this argument is similar to one made earlier in the paper, namely our insistence that rescue behavior need not involve intentionality to function as rescue (see Component 4, above). Dickinson and his colleagues (de Wit and Dickinson, 2009; Dickinson, 2011) propose two criteria for distinguishing between alternative explanations of motivated behavior, in this case what drives the behavior of rescuers.

According to Dickinson and his colleagues (de Wit and Dickinson, 2009; Dickinson, 2011), to determine whether or not a particular behavior is goal-directed researchers must show that the behavior is sensitive to the *current* status of the outcome. In other words, in the context of rescue, the behavior of the rescuer should adapt dynamically to the needs of the other individual. If, for example, the supposed victim is not actually in distress, then no such attempt to rescue should occur. The Bartal et al. (2011) study failed to include a control group in which the victim was placed in the tube, but was not in distress, as might have been done by anesthetizing a restrained animal, preventing it from making ultrasonic vocalizations, etc. This criterion, and the control group it demands, rules out a highly likely alternative explanation for the rats’ behavior, namely that individuals were acting simply to reduce their own distress. Ants provide a very useful comparison on this point: Ants, also social animals, are likely to have been driven to terminate the call-for-help because natural selection has primed their nervous systems to experience stress when the relevant receptors are activated, and to behave in such a way to reduce their own stress; ant rescuers need not understand or share the feelings of the other ant, as empathetically motivated behavior requires. Although the rat chocolate-sharing experiment was intended to show further signs of empathy—the rescuer not only released the victim but shared an especially attractive treat—sharing chocolate with a conspecific is a natural outcome of rats’ foraging behavior, in which members of the colony transfer important information about a food source by smelling it on another individual, by interacting with others that have returned from foraging, and by sharing that food (Galef and Giraldeau, 2001; Galef and Laland, 2005). In short, food sharing is part of rats’ behavioral ecology, which also does not require empathy to operate efficiently.

A second criterion proposed by Dickinson and co-workers (de Wit and Dickinson, 2009; Dickinson, 2011) is that the response must be instrumental in obtaining the goal. In

the case of what Bartal et al. (2012) call empathetically motivated helping behavior, the free rat should be sensitive to the causal relation between its response and the goal of aiding the victim: If, for example, the well-being of the victim would be increased by requiring the free rat to move away from the victim, the free rat should modify its behavior accordingly. Of course, approaching the victim is exactly what both ants and rats are required to do by the experimental protocol, a protocol that cannot rule out alternative explanations for what looks like “empathetically motivated helping behavior.”

In short, the Bartal et al. (2011) study is a clever, very persuasive report of what we would want to label rescue behavior, even if the authors themselves do not use that word, preferring empathy instead. What Bartal et al. (2012) have demonstrated is that, very much like ants, rats—a species in which individuals, in their natural habitat, form colonies, engage in cooperative behavior, and risk possible entrapment whenever they leave the nest in search of food—are highly likely to engage in rescue behavior.

### **Algorithms vs. Intentional Behavior**

If, in the absence of the kinds of controls described above, researchers insist on using the word empathy to describe rats’ motivation, then any study in which rescue behavior takes on the same appearance could legitimately be used as evidence of empathy. That is, there is no basis to deny that ants are empathetically motivated too, which given our understanding of evolution, is an absurd proposition. However, some researchers have adopted a very different approach to the study of empathy. That is, one might argue instead that empathy has been far too narrowly and mentalistically defined, involving complex cognitive capacities such as theory-of-mind (ToM) in which individuals possess the ability to understand another’s world-view (Goldman, 2006). For example, Baron-Cohen (2005) describes empathy as “a leap of imagination into someone else’s headspace” (p. 170). Alternatively, de Waal (2011) argues that empathy should be understood as an “umbrella term,” a label that encompasses multiple layers of ways in which animals might respond to the distress of others. According to this view, at the most basic level of empathy, an animal sees another individual’s emotional response and, via simple hard-wired mechanisms, experiences a similar state, which in turn generates a response that is similar to that experienced by the observed individual (Preston and de Waal, 2002). This kind of emotional contagion is likely widespread in many species, but does not involve “understanding” another’s emotional state in the mentalistic sense. The next level, called pre-concern, in which individuals approach and provide some form of comfort, also is relatively basic. As de Waal (2011) describes this level, “it is as if nature had endowed the organism with a simple behavioral rule: ‘If you feel another’s pain, get over there and make contact’” (p. 91). Presumably, because ants do not merely experience distress in the presence of an entrapped nestmate, but also “go over and make contact,”—contact that, on an operational level, resembles what rats do—ants’ rescue behavior would fall into this latter category. Finally, sympathetic concern and perspective taking are more advanced levels of de Waal’s (2011) model, which as the labels imply do indeed involve more complex cognitive mechanisms.

The advantage of this view of empathy is that it acknowledges the action of

evolution in two complementary ways. One, the model recognizes that the similarities and differences in the means through which both human and non-human animals attend to another's distress are necessarily the result of convergent and divergent selection processes. In other words, just because ants' and rats' rescue behavior appears similar, doesn't mean that it comes about via the same mechanism. Two, the ability to truly understand and react to another's distress most likely evolved from simpler forms, similar to Jacob's (1977) classic view of natural selection as an excellent "tinkerer, [who] gives his materials unexpected functions to produce a new object" (p. 1164).

We don't disagree; indeed, de Waal's Darwinian model (2011) has much merit. Nonetheless, if empathy—reacting to another's distress—can be understood to exist on many different levels, then we need methodologies to distinguish between them. Put another way, in the absence of rigorous definitions—and, even more importantly, control groups—that allow us to interpret behavior unambiguously, we cannot know whether rats "understand" another's distress and "intend" to rescue another individual any more than ants do. We find no value in an "umbrella term" if the various behavioral reactions encompassed under that umbrella cannot be distinguished from one another.

In interpreting the behavior of ant and rat rescuers, for example, a series of simple algorithms or "rules of thumb," including the "approach rule" proposed by de Waal (2011) and described above, could explain much of what appear to be a very complex series of events. That is, in both rats and ants, a call-for-help alarms conspecifics, producing frenetic movement in multiple directions as the rescuer attempts to orient toward the source. This call-for-help is a chemical signal, a pheromone, in many ants (Blum and Warter, 1966; Hangartner, 1969; Spangler, 1968; Wilson, 1958) and an auditory signal, namely ultrasonic vocalizations, in rats (Brudzynski and Ociepa, 1992), but the same argument can be made whatever the animal's sensory process. After the rescuer detects the source, it then simply follows the signal's sensory gradient—de Waal's "approach rule"—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 special combination of "call-for-help plus contact" releases hard-wired "rescue behavior": The rescuer digs and pulls.

We propose that further exploration of simple algorithms such as these can help researchers figure out what "more" is needed to explain the behavior of rescue behavior in distant taxa. For example, how do ants recognize what is holding the victim in place and direct their attention to this object in particular, even when other "non-ant objects" are in equally close proximity? How do rats learn to release the restrainer door? Would they learn to do so if the experimenters did not open the door first? Lest the behavior of rats seems more sophisticated in this regard than does the behavior of ants, we might add that, following futile attempts to bite through the snare holding their nestmate, we often observed that some ants crawled underneath the filter paper and bit at the knot instead, all the while ignoring the filter paper, although it, too, was in direct contact with the victim.

## **Conclusion**

A complete understanding of rescue behavior requires both proximate and ultimate

analyses (Tinbergen, 1963). At a proximate level, algorithms may take us much further in understanding rescue behavior than we might at first imagine, as we have tried to show by comparing ants' and rats' behavior. Indeed, algorithms can serve as important heuristic devices: Comparing rescue behavior in different species forces us to confront the possibility that equally simple, albeit different, proximate mechanisms may be at work. At an ultimate level, on the other hand, we have tried to show that rescue behavior appears to emerge in very distant taxa under similar conditions. In each case, individuals live in cooperative societies, depending on others in various ways, such as obtaining food and providing defense. In addition, these same individuals risk danger, which greatly affects the society as a whole. Although our study of rescue behavior still is woefully incomplete, the history of behavioral ecology suggests that that an algorithmic analysis at the proximate level, combined with a behavioral ecological approach at an ultimate level, is likely to provide a deep understanding of both the proximate and ultimate bases of rescue behavior.

**Acknowledgements:** We thank our co-authors: Jean-Luc Durand and Alexandra Scohier at Université Paris 13; Alex Kacelnik and Marco Vasconcelos at Oxford University; and, our student co-authors at Mount Holyoke College: Lauren Guillette, Audrey Markarian, Heather Cogswell, Kenzie Snyder, Katie Taylor and Allison Visvader. For access to Reserva Científica de Doñana and funding of the Spanish portion of the comparative study of ants project, we thank the ICTS-RBD Program, especially Xim Cerdá, Begoña Arrizabalaga and Rosa Rodríguez. Finally, support of our work was provided through a Faculty Grant from Mount Holyoke College (KLH), as well as from Laboratoire d'Éthologie Expérimentale et Comparée, Université Paris 13 (EN and KLH).

**Received 31 August 2012; Revision submitted 02 December 2012; Accepted 02 December 2012**

## References

- Baron-Cohen, S. (2005). Autism—"Autos": Literally, a total focus on the self? In T. E. Feinberg and J. P. Keenan (Eds.), *The lost self: Pathologies of the brain and identity* (pp. 166-180). Oxford: Oxford University Press.
- Bartal, I. B. -A., Decety, J., and Mason, P. (2011). Empathy and pro-social behavior in rats. *Science*, 334, 1427-1430.
- Beck, J., and Kunz, B. K. (2007). Cooperative self-defence: Matabele ants (*Pachycondyla analis*) against African driver ants (*Dorylus* sp.; Hymenoptera: Formicidae). *Myrmecology News*, 10, 27-28.
- Belt, T. (1874). *The Naturalist in Nicaragua*. London: Murray.
- Blum, M. S., and Warter, S. L. (1966). Chemical releasers of social behavior. VII. The isolation of 2-heptanone from *Conomyrma pyramica* (Hymenoptera: Formicidae: Dolichoderinae) and its modus operandi as a releaser of alarm and digging behavior. *Annals of the Entomological Society of America*, 59, 774-779.
- Brudzynski, S. M., and Ociepa, D. (1992). Ultrasonic vocalization of laboratory rats in response to handling and touch. *Physiology and Behavior*, 52, 655-660.



- Caro, T. M. (1994). *Cheetahs of the Serengeti plains*. Chicago: University of Chicago Press.
- Caro T. M., and Hauser, M. D. (1992). Is there teaching in nonhuman animals? *Quarterly Review of Biology*, 67, 151-174.
- Connor, R. C. (1995). The benefits of mutualism: A conceptual framework. *Biological Reviews*, 70, 427-457.
- Czechowski, W., Godzińska, E. J., and Kozłowski, M. W. (2002). Rescue behavior shown by workers of *Formica sanguinea* Latr., *F. fusca* L. and *F. cinerea* Mayr (Hymenoptera: Formicidae) in response to their nestmates caught by an ant lion larva. *Annales Zoologici*, 52, 423-431.
- Darwin, C. (1877). *On the various contrivances by which orchids are fertilised by insects* (5th ed.). New York: Appleton.
- Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.
- Dawkins, R. (1982). *The extended phenotype*. Oxford: Oxford University Press.
- de Waal, F. B. M. (2011). Empathy in primates and other mammals. In J. Decety and J. T. Cacioppo (Eds.), *The Oxford handbook of social neuroscience* (pp. 87-107). New York: Oxford University Press.
- de Wit, S., and Dickinson, A. (2009). Associative theories of goal-directed behaviour: A case for animal-human translational models. *Psychological Research*, 73, 463-476.
- Dickinson, A. (2011). Goal-directed behavior and future planning in animals. In R. Menzel and J. Fischer (Eds.), *Animal thinking: Contemporary issues in comparative cognition* (pp. 79-910). Cambridge, MA: MIT Press.
- Dugatkin, L. A. (1997). *Cooperation among animals: An evolutionary perspective*. New York: Oxford University Press.
- Forrest, H. F. (1963). *Three problems in invertebrate behavior. II. The digging out of trapped or buried ants by other workers*. (Unpublished doctoral dissertation). Rutgers University, New Brunswick, NJ.
- Galef, B. G., Jr., and Giraldeau, L. A. (2001). Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. *Animal Behaviour*, 61, 3-15.
- Galef, B. G., Jr., and Laland, K. N. (2005). Social learning in animals: Empirical studies and theoretical models. *Biological Sciences*, 55, 489-499.
- Goldman, A. (2006). *Simulating minds: The philosophy, psychology, and neuroscience of mindreading*. Oxford: Oxford University Press.
- Guillette, L., Hollis, K. L., and Markarian, A. (2009). Learning in a sedentary insect predator: Antlions (Neuroptera: Myrmeleontidae) anticipate a long wait. *Behavioural Processes*, 87, 224-232.
- Hamilton, W. D. (1963). The evolution of altruistic behavior. *American Naturalist*, 97, 354-356.
- Hamilton, W. D. (1964) The genetical evolution of social behavior I and II. *Journal of Theoretical Biology*, 7, 1-52.
- Hangartner, W. (1969). Carbon dioxide, a releaser for digging behavior in *Solenopsis geminate* (Hymenoptera: Formicidae). *Psyche*, 76, 58-67.
- Hölldobler, B., and Wilson, E. O. (1990). *The ants*. Berlin: Springer-Verlag.
- Hollis, K. L., Cogswell, H., Snyder, K., Guillette, L. M., and Nowbahari, E. (2011).

- Specialized learning in antlions, pit-dwelling insect predators, shortens vulnerable larval stage. *PLoS ONE*, 6, e17958.
- Hollis, K. L., and Guillette, L. M. (2011). Associative learning in insects: Evolutionary models, mushroom bodies, and a neuroscientific conundrum. *Comparative Cognition and Behavior Reviews*, 6, 24-45.
- Hollis, K. L., and Nowbahari, E. (2013). A comparative analysis of precision rescue behaviour in sand-dwelling ants. *Animal Behaviour*, 85, 537-544.
- Howard, R. W. (1993). Cuticular hydrocarbons and chemical communication. In D. W. Stanley-Samuelson and D. R. Nelson (Eds.), *Insect lipids: Chemistry, biochemistry and biology* (pp. 179-226). Lincoln, NE: University of Nebraska Press.
- Howard, R. W., and Blomquist, G. J. (2005). Ecological, behavioral, and biochemical aspects of insect hydrocarbons. *Annual Review of Entomology*, 50, 371-393.
- Jacob, F. (1977). Evolution and tinkering. *Science*, 196, 1161-1166.
- Kolm, N., Amcoff, M., Mann, R. P., and Arnqvist, G. (2012). Diversification of a food-mimicking male ornament via sensory drive. *Current Biology*, 22, 1440-1443.
- Kunz, T. H., Allgaier, A. L., Seyjagat, J., and Caligiuri, R. (1994). Allomaternal care: Helper-assisted birth in the Rodrigues fruit bat, *Pteropus rodricensis* (Chiroptera; Pteropodidae). *Journal of Zoology*, 232, 691-700.
- Lafleur, L. J. (1940). Helpfulness in ants. *Journal of Comparative Psychology*, 30, 23-29.
- Lehmann, L., and Keller, L. (2006). The evolution of cooperation and altruism: A general framework and a classification of models. *Journal of Evolutionary Biology*, 19, 1365-1376.
- Markl, H. (1965). Stridulation in leaf-cutting ants. *Science*, 149, 1392-1393.
- McEwen, B. S., and Seeman, T. (1999). Protective and damaging effects of mediators of stress: Elaborating and testing the concepts of allostasis and allostatic load. *Annals of the New York Academy of Science*, 896, 30-47.
- Nowbahari, E., and Hollis, K. L. (2010). Rescue behavior: Distinguishing between rescue, cooperation, and other forms of altruistic behavior. *Communicative and Integrative Biology*, 3, 77-79.
- Nowbahari, E., Hollis, K. L., and Durand, J.-L., (2012). Division of labor regulates precision rescue behavior in sand dwelling *Cataglyphis cursor* ants: To give is to receive. *PLoS ONE*, 7, e48516.
- Nowbahari, E., Scohier, A., Durand, J.-L., and Hollis, K. L. (2009). Ants, *Cataglyphis cursor*, use precisely directed rescue behavior to free entrapped relatives. *PLoS ONE*, 4, e6573.
- Preston, S. D., and de Waal, F. B. M. (2002). Empathy: Its ultimate and proximate bases. *Behavioral and Brain Sciences*, 25, 1-72.
- Sapolsky, R. M. (1996). Stress, glucocorticoids and damage to the nervous system: The current state of confusion. *Stress*, 1, 1-16.
- Siebenaler, J. B., and Caldwell, D. K. (1956) Cooperation among adult dolphins. *Journal of Mammalogy*, 37, 126-128.
- Spangler, H. G. (1968). Stimuli releasing digging behavior in the western harvester ant (Hymenoptera: Formicidae). *Journal of the Kansas Entomological Society*, 41, 318-323.

- Taylor, K., Visvader, A., Nowbahari, E., and Hollis, K. L. (2013). Precision rescue behavior in North American ants. *Evolutionary Psychology*, *11*, 665-677.
- Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, *20*, 410-433.
- Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, *46*, 35-57.
- Vasconcelos, M., Hollis, K., Nowbahari, E., and Kacelnik, A. (2012). Pro-sociality without empathy. *Biology Letters*, *8*, 910-912.
- Vogel, E. R., and Fuentes-Jiménez, A. (2006). Rescue behavior in white-faced capuchin monkeys during an intergroup attack: Support for the infanticide avoidance hypothesis. *Journal of Primatology*, *68*, 1012-1016.
- Wilkinson, G. S. (1984). Reciprocal food sharing in the vampire bat. *Nature*, *308*, 181-184.
- Wilkinson, G. S. (1990). Food sharing in vampire bats. *Scientific American*, *262*, 76-82.
- Wilson, E. O. (1958). A chemical releaser of alarm and digging behavior in the ant *Pogonomyrmex badius* (Latreille). *Psyche*, *65*, 41-51.