Rescue behavior

Distinguishing between rescue, cooperation and other forms of altruistic behavior

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Reports of rescue behavior in non-human animals are exceedingly rare, except in ants where rescue is well known, but has not been explored experimentally until recently. Although we predict that rescue behavior should be limited to circumstances in which the victim and the rescuer are highly related to one another, or in which unrelated individuals must cooperate very closely with one another, we also predict that it is likely to be far more common than the current literature would suggest. To address this oversight, we propose a rigorous definition of rescue behavior, one that helps researchers to focus on its necessary and sufficient components, at the same time that it helps to differentiate rescue behavior from cooperation and other forms of helping behavior. In this way we also hope to expand our understanding of altruism in particular and kin selection in general.

In an article describing our recent work¹ on ant rescue behavior, Dugatkin was quoted as saying, "While researchers in the area of behavior and evolution have long studied altruism, controlled experimental work on rescue behavior is very rare... [suggesting] that we may be underestimating the extent of rescue behavior in the wild."² We agree that rescue behavior is likely to be far more prevalent than the paucity of current reports might suggest. Moreover, we believe that this oversight stems from lack of a formal, operational definition of rescue, one that clearly differentiates it from other forms of altruistic behavior but, at the same time, recognizes its theoretical links to altruism in particular and kin selection theory in general.³⁻⁶ Here we attempt to formulate such a definition of rescue behavior.

Briefly, we propose that rescue behavior involves four components that, taken together, are necessary and sufficient for a behavior to be labeled rescue: (1) The victim is in distress; (2) the behavior of the rescuer is suited to the circumstances of the victim's distress; (3) the rescuer places itself at risk by engaging in rescue behavior; and, finally, (4) the act of rescuing is not inherently rewarding or beneficial to the rescuer. Each of these

*Correspondence to: Karen L. Hollis; Email: khollis@mtholyoke.edu Submitted: 09/05/09; Accepted: 09/05/09 Previously published online: www.landesbioscience.com/journals/cib/article/10018 components is discussed in detail below, wherein we elaborate on both the definitional and theoretical parameters.

Component 1: The Victim is in Distress

By distress, we mean that the victim must be in a situation that poses an immediate physical risk to itself, such that, if it is not rescued or does not escape the current situation, it will suffer severe physical harm. This restriction to situations involving physical harm helps to differentiate rescue behavior from situations involving other fitness costs: Female Rodriques fruit bats assist pregnant conspecifics in the birthing process,⁷ cooperative behavior that likely results in easier deliveries; however, under normal circumstances, the mother is not in danger of severe physical harm. A cub about to wander too close to a predatory snake may be rescued by a parent. However, that same parent is not said to rescue its offspring if it delivers food when the offspring is hungry or if it somehow prevents its offspring from engaging in behavior that is merely energetically costly, as when that parent helps to improve the cub's predatory abilities.8 Although shortterm metabolic costs certainly represent reductions to fitnessand although a victim in real distress may indeed accrue such costs as it attempts to escape the distressful situation-short-term metabolic costs and other such forms of fitness costs are, in themselves, neither necessary nor sufficient to define distress.

Nonetheless, our definition of "physical" is not as limited as it might at first appear. The physical consequences of the distressful situation can be direct, when, to use our own work as an example, an ant is ensnared by an inanimate object from which it cannot escape and thus would die if not rescued.¹ Alternatively, the physical consequences can be indirect; we advocate that indirect consequences be included to provide a more comprehensive definition of rescue. To use a human animal example, individuals often are said to rescue others from an ongoing and severe stressful situation by removing or attenuating that stress in some way, as when a woman is rescued from an emotionally abusive partner by others who provide an alternative place to live. Although chronic stress does not produce immediate and direct physical harm, it is widely understood to produce a cascade of deleterious physical and genetic changes via the endocrine system.⁹⁻¹¹ In short, then, for a behavior to be called rescue, the victim must

be in a situation that risks or incurs physical harm, a fitness loss that is severe.

This physical distress component is the only one, we propose, that focuses directly on the victim and its behavior. Although many cases of rescue behavior are characterized by a call-for-help, released by the victim and detected by potential rescuers,¹²⁻¹⁶ we do not propose that communication is a necessary part of all rescue behavior. Certainly, the call-for-help is a fascinating and well-studied addition to rescue behavior; moreover, it may indeed be necessary in some animals, for example, ants.¹²⁻¹⁶ However, rescue attempts, at least by human animals, may be made in the absence of such calls, which leaves open the possibility that the same is true in other species. Thus, although a call-for-help may be necessary to elicit rescue in some animals—indeed, it may constitute the means whereby individuals recognize that another individual is in distress—the eliciting stimulus does not need to be a necessary part of the definition of rescue behavior.

In a similar vein, rescue behavior may or may not require that individuals recognize one another individually, recognize related individuals, or recognize members of the same species. For example, in our paper on ant rescue behavior, we show that *Cataglyphis cursor* ants do not rescue individuals from another colony of the same ant species, thus demonstrating that ants must be able not only to recognize distress, but also to recognize colony members and distinguish them from non-relatives.¹ Here, too, however, whatever are the underlying cognitive mechanisms required for individual recognition, kin recognition or species recognition, they are not required in all cases of rescue behavior and, thus, we do not propose to make them part of the definition of rescue behavior.

Component 2: The Rescuer Places itself at Risk by Engaging in a Rescue Attempt

This component of rescue behavior, as well as Component 4, in which we argue that the rescuer gains no reward or benefit from the act of rescuing, not only go hand in hand, but also mark rescue behavior as a special case, an extreme form, of altruism. In limiting rescue behavior in this way, we intend to reserve it for a special place along a continuum of helping behavior, for which the extremely high costs and non-existent rewards make it one that would be predicted to occur, according to kin selection theory,^{3,4} only when individuals are highly related to one another, or in societies in which individual fitness necessitates that individuals cooperate very closely with one another.³⁻⁶

Concerning the risk to the rescuer, more often than not that risk is the very one shared by the victim: Ants that rescue a nestmate entrapped under fallen debris,¹ or caught in an antlion's pit,^{17,18} easily might become entrapped or caught themselves; a single male capuchin monkey that rescues a female and her infant by driving away six male attackers from another group¹⁹ certainly risks injury to itself; and, dolphins that surround a pod member injured in a fishing operation, and then lift it to the surface so that it can breathe,²⁰ risk similar injury themselves.

The report of the injured dolphin,²⁰ the first of only two reported cases of rescue in vertebrates, describes other instances of this same behavior and, in so doing, necessitates that we address an important theoretical issue. The authors themselves refer to the behavior in question as "cooperation" and, in addition to the example of what we propose, instead, to call rescue behavior, they refer to reports of this "same behavior" performed by mothers who lift and support their infants to the surface. Although we agree that the motor behavior is identical, we would argue that dolphin mothers are performing altruistic acts vis á vis their infants, but dolphins that place themselves at risk to aid an injured member of their pod are engaged in rescue behavior. Our focus on the function of rescue behavior-to remove a distressed victim from physical harm at great cost to the rescuer and without reward-rather than on shared motor pathways, is similar to the way in which animal behavior researchers approach other kinds of behavior,²¹ for example, territorial aggression, foraging, migration, reproductive behavior and more recently, play behavior.²² By focusing on the function, we seek to differentiate rescue from other forms of altruism.

Component 3: The Behavior of the Rescuer is Generally Suited to the Circumstances of the Victim's Distress

Because not all rescue attempts are successful, we must be careful to define rescue behavior independently of its outcome. In addition, if the definition is to be generalizable, and thus applied to ants, monkeys, dolphins and humans alike, then it must avoid reference to "intentionality" on the part of the rescuer: Pulling on the limbs of an ensnared nestmate and, even, biting at the nylon snare itself, does not require that an ant "intends" to release the victim, nor does it require that the ant "recognizes" 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 mere presence of a individual (the victim) serves as a releaser for behavior that is not relevant to the circumstances, we propose that the behavior of the rescuer be somehow relevant to the circumstances of the victim's distress. Of course, relevance may be in the eyes of the beholder, and we recognize the ambiguity of this definitional component-but, minimally, it helps to eliminate instances when, for example, a victimized adult is approached by its offspring seeking food.

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 benefit that accrues from kin selection or reciprocal altruism^{3-6,23-26}—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, in which individuals engage concurrently in behavior that benefits all parties simultaneously.⁵⁻ ^{6,23-25}

An example of this form of cooperation, which underscores the importance of a rigorous definition of rescue behavior, is a case reported by Beck & Kunz,²⁷ 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 individuals sometimes turned back to attack a driver ant attacking a conspecific, an act that might at first appear to be rescue behavior. However, it's 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? Although an anonymous reviewer of our PLoS ONE article1 requested that we acknowledge the Beck & Kunz paper as a case of rescue behavior, we felt strongly that it was important to reject this argument: We agree that the report was a cleverly designed field experiment, and we cite it for that reason; however, 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. Rescue behavior is both fascinating and rare, precisely because there is not an immediate direct benefit to the rescuer.

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 & Hauser²⁸ 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".²⁹ However, there are many unsung heroes in our midst: Most instances of rescue behavior, like good teaching, go unrewarded—and yet the behavior persists.

Rescue Behavior: A Summary

We propose that, taken together, four components of rescue behavior distinguish it from other forms of helping behavior and that these four components are necessary and sufficient to define rescue. One, the individual-to-be-helped is in distress, meaning that, unless it escapes on its own, or is removed from the circumstances, it will suffer, or will continue to suffer, severe physical harm. Two, the rescuer places itself at risk by engaging in a rescue attempt. Three, the behavior of the rescuer is generally suited to the circumstances of the victim's distress. Finally, four, the act of rescuing is not inherently rewarding or beneficial to the rescuer. By defining rescue in a way that distinguishes it from other forms of helping behavior, we hope to raise awareness of this fascinating form of behavior and encourage its study in many more animals, vertebrates and invertebrates alike.

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