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What is Rescue Anyways? A Comprehensive Review of Rescue and Rescue Adjacent Behavior Across Taxa

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Abstract – The term "rescue behavior" refers to a special form of altruism in which an individual aids another individual currently in distress or danger, with no obvious direct benefit to itself. In this review, we develop a modified version of Nowbahari and Hollis' (2010) rescue criteria to classify the existing literature on rescue behavior. We aim to identify what taxa perform rescue or rescue-like behaviors, and quantify the hypothesized drivers of these behaviors. We propose novel criteria for evaluating rescue in further studies, and classify the existing literature into three groups based on this modified criteria. We suggest that many behaviors are excluded from the existing literature on rescue because they are instead studied and discussed under different terminology. Thus, rescue behavior may be more common than previously thought. However, a key component of rescue is risk, which can be difficult to assess. More work is needed to integrate how we think about and assess risk, and how we define rescue behavior.

Keywords – Altruistic behavior, Cooperation, Prosocial behavior, Rescue behavior

Altruistic behavior is when one individual assists another individual while incurring costs to itself (Hamilton, 1964). Altruism is found widely in the animal kingdom from invertebrates, like ants (*Cataglyphis cursor,* Nowbahari & Hollis, 2009) and aphids (*Pemphigus spyrothecae,* Foster, 1990), to vertebrates, like dolphins (*Tursiops truncatus*, Siebenaler & Caldwell, 1956) and rodents (*Rattus norvegicus,* Carvalheiro et al., 2019). Kin selection, one driver of altruistic behavior, refers to an animal engaging in altruistic behavior that benefits the genetic fitness of its relatives, in this review, kin selection indicates indirect fitness specifically (West et al., 2007). Here, reciprocal altruism refers to altruism that occurs between unrelated individuals where there is an expectation of repayment or the promise of repayment of the altruistic act in the future (Trivers, 1971).

Altruism, as applied by Hamilton (1964), involves evaluating the cost to benefit ratio of the action, and the relatedness of the actors. Further theories involve cost/benefit analyses in the case of non-related actors (Trivers, 1971). Cooperative antipredator behavior, where two or more individuals work together to deter predation, can be altruistic, particularly in Trivers' reciprocal altruistic sense (Krams et al., 2008; Stenstrom et al., 2026). Determining the costs and benefits to each actor in these scenarios is quite difficult, and Nowbahari and Hollis (2010) discuss how teasing apart self-defense behaviors and other-defense behaviors is nearly impossible. Long-term expectations of reciprocity are also nearly impossible to quantify, especially in the lens of rescue behavior, which is typically studied in one-off incidents.

Rescue behavior is a form of altruism that is primarily studied experimentally in rodents and eusocial insects. Before 2010, rescue was rarely studied outside of eusocial insects and humans. Considering rescue behavior in different animals is a fairly recent area of study (e.g., Ben-Ami Bartal et al., 2011; Hammers & Brouwer, 2017; Masilkova et al., 2021; Nowbahari & Hollis, 2010). Species that have been observed or tested for rescue behavior are those that typically live in stable groups (e.g., eusocial insects, rodents, dolphins), provide parental care or care for the young (all the bird species present in the literature, dolphins, whales, non-human primates, eusocial insects), and have some kind of social hierarchy (e.g., non-human primates, eusocial insects, dolphins). Understanding what constitutes rescue behavior across taxa is essential to understanding what ecological, evolutionary, and social conditions are associated with rescue behavior as a whole, and if there is a general "profile of a rescuer" that should be considered when studying rescue behavior and its components.

There are few experimental studies on rescue or rescue-like behavior outside of eusocial insects (Frank et al., 2017; Nowbahari et al., 2009) and rodents (Quinn et al., 2018; Sato et al., 2015). Most of the published literature for rescue behavior is either observational (Kuczaj et al., 2015; Masilkova et al., 2021) - containing some evidence of the behavior such as photos or videos - or purely anecdotal, even if this anecdote was acquired during the course of regular research (e.g., Eberle & Kappeler, 2008; Vogel & Fuentes-Jimenez, 2006).

Here, we review the current literature on rescue behavior, focusing on two main factors. We describe the taxa in which rescue is either documented or experimentally tested, as well as what the authors of the literature propose motivates rescue behavior. We then assess the generalizability of Nowbahari and Hollis' (2010) definition of rescue.

Methods

Search Protocol

We used the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Moher et al., 2009) to inform the flow of information reporting for this review. We used the Handbook of Meta-analysis in Ecology and Evolution to acquaint ourselves with the methodology used in these kinds of systematic reviews (Koricheva et al., 2013).

We conducted our search in three different databases: Web of Science, Scopus, and PsychInfo OVID. We used the terms "rescue behavior," "altruistic behavior," "prosocial behavior," and "helping behavior" to start broadly (for a full list of search terms see Table 1).

After observing that within rodent studies rescue was more loosely defined, we also conducted a search on "rodent door opening behavior" and "rodent prosocial behavior." We also conducted a search on "agonistic support," which is where an individual helps a groupmate in conflict by attacking the groupmate's opponent. However, this search was terminated in short order as we largely found evidence that agonistic support is not risky for the "rescuer," and it may actually benefit the "rescuer" or supporting actor (Chapais et al., 1991; Pallante et al., 2016; Shino & Aureli, 2009; but see Fraser & Bugnyar, 2012).

Table 1

A List of the Search Terms and Databases Used

Database	Search Term	Records Returned
Web of Science (All Databases)	((((TS=("rescue behav*" OR "altruis*")) AND TS=("rescue" OR "altruis* behav*" OR "help* behav"))) NOT TS=("socioeconom*" OR "student" OR "human" OR "cooperative breeding" OR "search and rescue" OR "allo*" OR "rehab*" OR "rescue cent*" OR "rescue mission" OR "rescue operation" OR "shelter" OR "gene* rescue" OR "molecul* rescue" OR "dna" OR "rna" OR "virus" OR "protein"))	1,203 Results
Scopus	ALL ("rescue behav*" OR "rescue") OR ("altruis* behav*") AND ("animal" OR "nonhuman") AND NOT ("cooperative breed*" OR "communal breed*" OR "search and rescue" OR "allo*" OR "rehab*" OR "rescue cent*" OR "rescue mission" OR "rescue operation" OR "shelter" OR "gene* rescue" OR "molecul* rescue" OR "dna" OR "rna" OR "virus" OR "protein" OR "plants" OR "trees" OR "botany" OR "soil eco*" OR "soil" OR "human" OR "child*" OR "volunteer*" OR "alarm* call*" OR "breeding help*" OR "conservation effort*" OR "questionnaire" OR "survey" OR "helper at the nest" OR "food shar*" OR "token task" OR "math* model" OR "model" OR "pop* gen*") AND (LIMIT-TO (DOCTYPE , "ar")) AND (LIMIT-TO (SUBJAREA , "AGRI") OR LIMIT-TO (SUBJAREA , "SOCI") OR LIMIT-TO (SUBJAREA , "MULT") OR LIMIT-TO (SUBJAREA , "PSYC") OR EXCLUDE (SUBJAREA , "BIOC") OR EXCLUDE (SUBJAREA , "ENVI") OR EXCLUDE (SUBJAREA , "ARTS") OR EXCLUDE (SUBJAREA , "IMMU") OR EXCLUDE (SUBJAREA , "MEDI") OR EXCLUDE (SUBJAREA , "ENGI") OR EXCLUDE (SUBJAREA , "ECON") OR EXCLUDE (SUBJAREA , "BUSI") OR EXCLUDE (SUBJAREA , "COMP") OR EXCLUDE (SUBJAREA , "HEAL") OR EXCLUDE (SUBJAREA , "CHEM") OR EXCLUDE (SUBJAREA , "DECI") OR EXCLUDE (SUBJAREA , "MATH") OR EXCLUDE (SUBJAREA , "NURS") OR EXCLUDE (SUBJAREA , "PHAR") OR EXCLUDE (SUBJAREA , "PHYS")) AND (LIMIT-TO (LANGUAGE , "English"))	222 Results
PsychInfo	"rescue behav*" limit to (peer reviewed journal and animal and "0110 peer-reviewed journal" and journal article and animal)	46 Results
Web of Science (All databases)	(TS=(rodent door opening OR door opening behav*)) NOT TS=("alzh*" OR "dement*" OR "environmental science" OR "energy" OR "agriculture" OR "survey" OR "hen*" OR "aging" OR "sleep*" OR "pest" OR "pest manage*" OR "problem solving task" OR "explore*" OR "map*" OR "spatial map*" OR "cell" OR "computer" OR "model" OR "blood" OR "memor*" OR "maze" OR "gene* rescue" OR "food sharing" OR "maternal" OR "molecular" OR "sexual behavior" OR "copulat*" OR "mental health" OR "healthcare" OR "engineer*") and Humans or Middle Aged or Child or Surveys And Questionnaires or Child Preschool or Photic Stimulation or Aged 80 And Over or Polymers or Schizophrenia or Air Pollution Indoor or Hiv Infections or Nanoparticles or Alzheimer Disease or History 20th Century or Schizophrenic Psychology or Particle Size or Imaging Three Dimensional or Hospitalization or Pregnancy or Environmental Exposure or Commitment Of Mentally Ill or Cell Survival or Cell Differentiation or Cell Culture Techniques or Blood Brain Barrier or Cats or Child Development or Cell Line Tumor or Antineoplastic Agents or Anopheles or Sexually Transmitted Diseases or Biocompatible Materials or Sars Cov 2 or Health Personnel or Health Services Accessibility or Models Theoretical or Ventilation or Covid 19 or Attitude To Health or Water or Violence or Suicide or Socioeconomic Factors or Interprofessional Relations or Mosquito Control or Nanotechnology or Obesity or Patient Safety or Referral And Consultation or Interviews As Topic or Internet or Dose Response Relationship Drug or Primary Health Care or Quality Of Life or Rural Population or Security Measures or Cognitive Behavioral Therapy or Consumer Behavior or Metal Nanoparticles or Mental Health Services or Mental Health or Longitudinal Studies or Inpatients or Infant Newborn or Drug Carriers or Delivery Of Health Care or Health Knowledge Attitudes Practice or Health Promotion or Substance Related Disorders or Cells Cultured or Biomarkers or Attitude Of Health Personnel or Surface Properties or Tissue Engineering (Exclude – MeSH Headings) and Behavioral Sciences or Zoology or Environmental Sciences Ecology or Psychology or Veterinary Sciences or Reproductive Biology or Entomology or Evolutionary Biology or Developmental Biology (Research Areas) and Article (Document Types) and Physiology (Exclude – Research Areas)	199 Results

Web of Science (All databases)	(TS=(empathy in rodent OR rodent empath* AND "rescue")) Search performed Jan 16, 2023 List auto-updated by database server on Jan 27, several papers removed by database. Only one had been considered relevant and remained in final analysis (Wu and Hong 2022	267 Results
Scopus	ALL ("rescue behav*" OR "rescue") OR ("altruis* behav*" OR "door opening" OR "empathy") AND ("rat" OR "rodent") AND NOT ("clinical" OR "cancer" OR "carcinoma" OR "cell*" OR "cooperative breed*" OR "communal breed*" OR "search and rescue" OR "allo*" OR "rehab*" OR "rescue cent*" OR "rescue mission" OR "rescue operation" OR "shelter" OR "gene* rescue" OR "molecul* rescue" OR "dna" OR "rna" OR "virus" OR "protein" OR "plants" OR "trees" OR "botany" OR "soil eco*" OR "soil" OR "human" OR "child*" OR "volunteer*" OR "alarm* call*" OR "breeding help*" OR "conservation effort*" OR "questionnaire" OR "survey" OR "helper at the nest" OR "food shar*" OR "token task" OR "math* model" OR "model" OR "pop* gen*") AND (LIMIT-TO (DOCTYPE , "ar"))	124 Results
PsychInfo	((("rescue behav*" or "rodent door opening" or "empathy") and "rodent") not "cell" not "cancer" not "memor*").mp. [mp=title, abstract, heading word, table of contents, key concepts, original title, tests & measures, mesh word]	22 Results
Web of Science	"agonistic support" (Topic) and Preprint Citation Index (Exclude – Database) and Article (Document Types)	103 Results

Inclusion/Exclusion Criteria

We searched the published literature through Web of Science, Scopus, and PsychInfo, and included peer-reviewed journal articles only. Only full text, English language articles were considered. The subject of the study had to be non-human animals, though studies involving domesticated animal-human dyads were included if the animal was the one performing the rescue behavior and was not involved in a search and rescue mission. With the exception of Carballo et al. (2020), which compares untrained dogs to military trained search and rescue dogs, search and rescue missions were excluded because these animals are specially trained to perform rescue-like behaviors in variable contexts.

We accepted three types of articles on rescue behavior, articles which tested/observed rescue behavior or behavior close to rescue, articles which used the term rescue behavior and met at least two of the criteria below, and review or opinion articles on rescue behavior.

We slightly altered Nowbahari and Hollis' (2010) rescue criteria for the following review:

1. The victim must be endangered or in distress.
2. The rescuer must put itself in *immediate* or *imminent* risk by engaging in a rescue attempt.
3. The behavior of the rescuer must be suited to the circumstances of the victim's distress.
4. There must be no inherent reward or benefit to the rescuer (except kin selection/reciprocal altruism).

During a preliminary literature review, we found that the "rescuer at risk" criteria was difficult to evaluate with only a basic understanding of many of the study systems present, or the literature on whether a risk was present was divided or unclear. Short-term risks (such as being captured by the same threat as the victim) were easier to identify than longer-term risks (both direct and indirect fitness costs, or cascading effects). Although we modified their criteria for this scoping review, we agree with Hollis and Nowbahari (2010) that having the rescuer at risk is valuable when evaluating systems and species in which the examining author is familiar or during experimental procedures. These modified criteria will be referred to as the Immediate Risk Rescue Criteria moving forwards.

Article Categorization

We categorized articles in the following manner: "True rescue" behaviors contained all of the Immediate Risk Rescue Criteria. "Rescue-adjacent" behaviors contained any three of the Immediate Risk Rescue Criteria. "Prosocial" behaviors contained any two of the Immediate Risk Rescue Criteria and the author used the term rescue and/or used methods consistent with rescue without assessing for a confounding social factor. "Responses/anti" papers were either published in direct response to another paper present in

the study or set out to test rescue and found results inconsistent with rescue/rescue-adjacent behavior. "Anti" papers are also referred to as "rescue-contesting." "Reviews" were papers containing and comparing rescue in multiple species, sought to review the literature surrounding rescue on a certain subject, or discussed the evolution of rescue or rescue itself as the subject.

We argue that the distinction between "true rescue" and "rescue-adjacent" behaviors is necessary so as to not disqualify systems in which rescue behavior may be present, but has either not been directly tested under a rescue hypothesis or systems that require a thorough cost-benefit analysis. Use of the modified criteria also allowed us to identify systems where rescue is almost certainly present, either because it has been directly tested under a rescue hypothesis, or the risks and benefits to the rescuer are obvious.

Unless otherwise stated by the authors, being in a restraining device (defined here as any object used to restrict the movement of the trapped animal) was considered "distressing" for the animals (e.g., rats or mice; Ben-Ami Bartal et al., 2011). Unless otherwise stated by the authors, being restrained in sand or introduced to a predator (e.g., an ant lion) was considered "distressing" or "endangering" for ants (Nowbahari and Hollis, 2013a).

We assessed whether or not the rescuer was at risk in terms of immediate risks and imminent risks. If short term (immediate) risks to the rescuer were not included, but are obvious by the nature of the rescue the "rescuer at risk," the requirement was considered fulfilled. For example, a dolphin bringing a stunned or injured pod member to the surface to breathe must temporarily risk suffocation or drowning and expends a great deal of time and energy while focused on helping the victim (Connor & Norris, 1982; Kuczaj et al., 2015). The rescuers may spend a significant length of time supporting the victim's breathing (Conner & Norris, 1982). When whaling practices were widespread and legal, whalers would take advantage of this behavior and the related "stand-by" behavior, where other pod members remain in a potentially dangerous area, to capture entire pods (Conner & Norris, 1982).

A longer term (imminent) example of risk is present in the case of humpback whales. While it is heavily contested whether mammal-eating orcas are capable of hunting and killing a healthy adult humpback whale, juveniles and subadults are known targets of orca attacks (Pitman et al., 2017). Humpback whales have been known to spend up to seven and a half hours disrupting a pod of orcas feeding (Pitman et al., 2017). Additionally, in cases where humpbacks approached orcas, 87% of the time the orcas were pursuing or actively eating prey - before the humpbacks arrived and disrupted this behavior (Pitman et al., 2017). While some time and energy expenditure is expected from any kind of helping behavior, we argue that humpback whales spending such extreme amounts of time and energy interrupting orcas constitutes rescue behavior.

If the risk is not short term, or obvious and not explained as putting the rescuer at risk, then this requirement was not considered fulfilled. For example, a rat touching a sensor or pushing a light lever to free a conspecific does not (under normal conditions) cause the rescuer to expend a considerable amount of energy or put itself at risk of injury or death by assisting a conspecific. In the case of the rat, the "rescuer at risk" requirement was not fulfilled (Ben-Ami Bartal et al., 2011, 2014, 2016; Cox & Reichel, 2019; Kalamari et al., 2021; but see Carvalheiro et al., 2019).

Articles were sorted by taxonomic order. Once there were four articles for a particular order, the group was created. Any orders with fewer than four records were sorted into the "Other" category under order. Review papers and rescue-contesting papers were not sorted into orders but were assessed separately.

Motivators

Motivators (defined here as factors that could potentially influence an individual to perform rescue behavior) were quantified if the author of the article detailed them explicitly. Motivator categories were created once four or more papers suggested a particular motivator. The motivators we considered are as follows: kin selection (referring to indirect fitness), reciprocal altruism, colony defense/maintenance, emotional contagion/perception action model, antipredator defense, empathy, prosocial behavior, and "other." If an author hypothesized that more than one motivator could be at play, each individual motivator

was counted only once in its respective category. "Other" refers to motivators that were listed three or fewer times.

Reviews and Rescue-Contesting

We considered reviews and rescue-contesting articles separately from empirical/observational journal articles. Reviews were not assessed for taxonomic groups, but were used to define terms or evaluate methods that could be used for behavioral experiments testing for rescue behavior with chickadees. Reviews were also used to locate primary sources, though due to the limited amount of literature on rescue behavior, these sources were often already acquired during our database searches.

Rescue-contesting articles were not assessed by taxa, as all of them focused on rodents. Three of these rescue-contesting behavior articles were in response to articles that argued for rescue behavior, and seven of them set out to test rescue themselves and found results inconsistent with rescue or rescue-adjacent behavior. These rescue-contesting papers were primarily used to evaluate methods and create the category of "prosocial behavior"- due to the potential confounder of social contact.

Results

PRISMA Search

A total of 1,816 results were returned from all searches; Figure S1 outlines how many articles were present at each step of the PRISMA process. Of the database searches, 113 articles were added to marked lists to be assessed for relevance. Two papers were removed for an inability to find a full-text English article. Ten of the remaining 111 articles were discarded for irrelevance (i.e., testing if a drug "rescues" behavior), one was discarded for incorrect document type (book). Once duplicates were removed, there were 74 total articles included in our analysis. One article (Pitman et al., 2017) was listed as both review and true rescue because it contains observational reports of rescue and self describes as a review. Of these articles, 30 met all of the revised rescue criteria and are listed as "true rescue." True rescue articles were almost equally experimental and observational, with 15 experimental articles, 14 observational articles, and one article that contained both experimental and observational components. Sixteen articles were listed as "rescue adjacent." The majority (15) of the rescue adjacent articles were experimental, and the remaining article was observational. There were 18 "prosocial behavior" articles, and 10 "responses/anti," all experimental. Lastly, there were 10 reviews, nine of which contained no experimental or observational component, and the remaining one contained an observational component. Of the 74 non-review articles, 58 were experimental (78%), 15 were observational (20%), and one contained both experimental and observational components (1%).

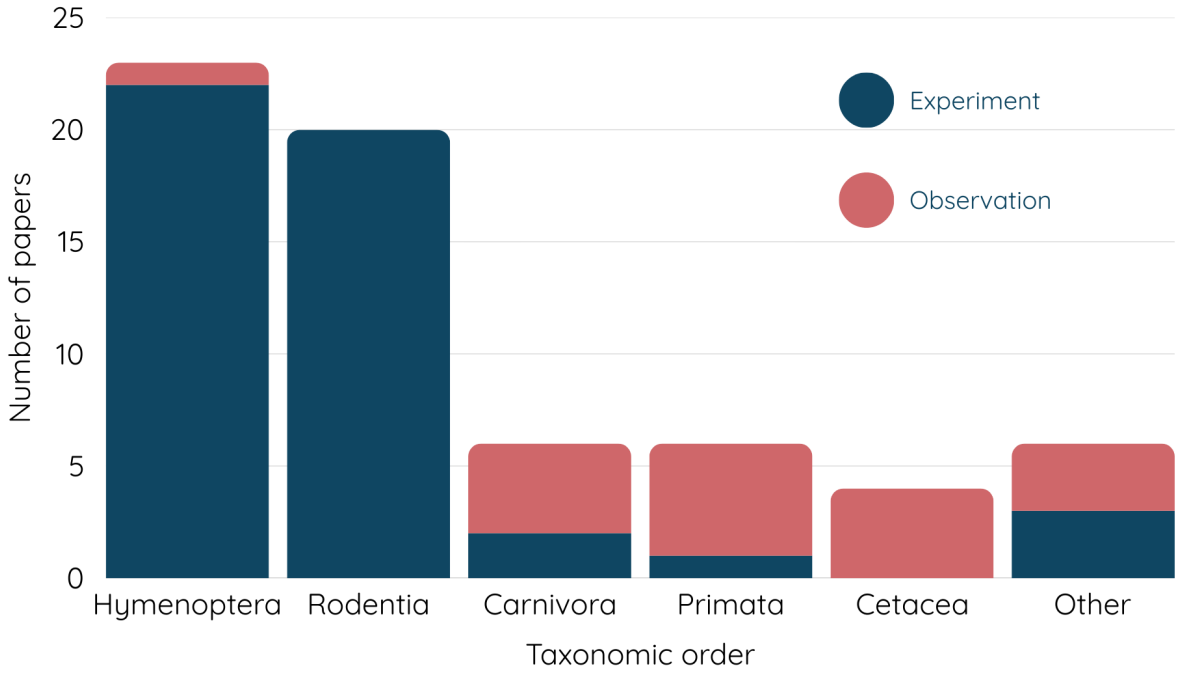
Records by Order

Of the 74 total records included in this analysis, the order Hymenoptera (i.e., wasps, bees, and ants) was the most prevalent (23 records, 22 of which were experimental, and one which contained both experimental and observational components), followed by Rodentia (i.e., rats and mice; 20 records, all experimental). Carnivora (i.e., mongooses and dogs) had six records (four observational, two experimental). Non-human primates (i.e., lemurs and capuchins) had five records (four observational, one experimental) and Cetacea (i.e., whales, dolphins, and porpoises) had four records, all observational. Six records were classified as "other" and contained orders Hemiptera (two, both experimental), Passeriformes (two, both observational), Artiodactyla (one, observational), and Chiroptera (one, experimental; Figure 1).

There were nine orders total. Of the 10 review articles, five were about Hymenoptera, one on Rodentia, one focused specifically on rats, and one focused specifically on Humpback whales. The remaining two reviews were not species specific. All of the responses/anti rescue articles were classified as Rodentia.

Figure 1

Records Returned by Order



Note. Number of records returned for rescue behavior searches per order, not included review or response/rescue-contesting articles. Hymenoptera (n=23), Rodentia (n=20), Carnivora (n=6), Primates (n=5), Cetacea (n=4), Other (n=6).

Rescue vs. Rescue-Adjacent

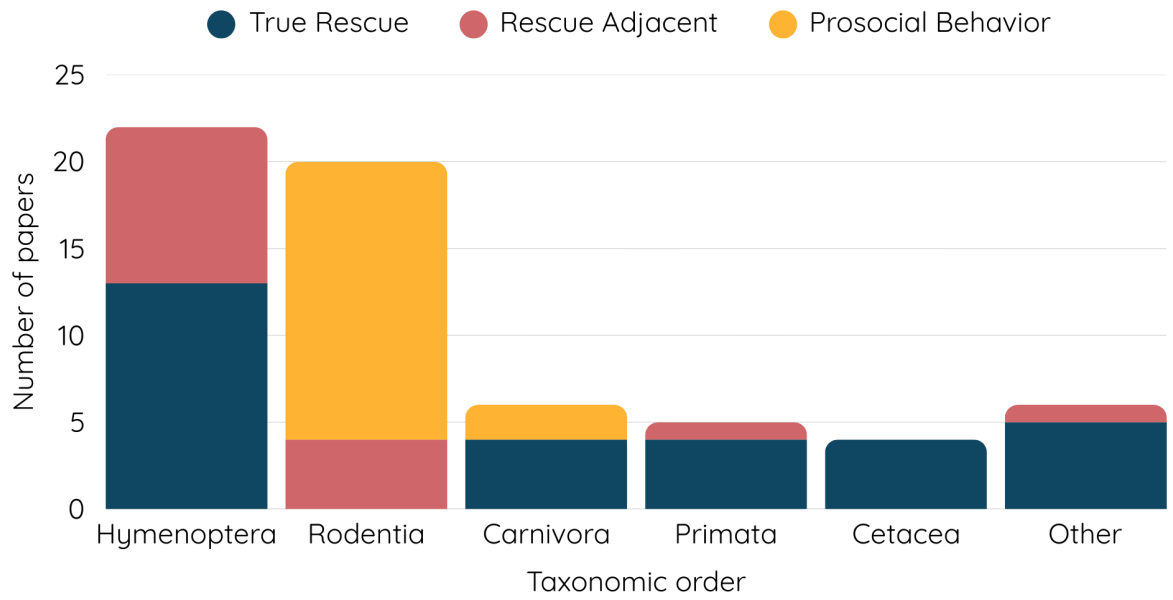
According to our analysis, true rescue behavior is seen in eight different orders: Hymenoptera (13/22 records), non-human primates (4/5 records), Cetacea (4/4 records), Carnivora (4/6 records), Artiodactyla (one wild boar, *Sus scrofa*), Hemiptera (two aphid species), Chiroptera (one vampire bat, *Desmodus rotundus*), and Passeriformes (one Seychelles warbler, *Acrocephalus sechellensis*). Rescue adjacent behavior is seen in Rodentia (3/20 records), Primata (one common marmoset, *Callithrix jacchus*), Hymenoptera (9/22 records), and Passeriformes (one Australian magpie, *Gymnorhina tibicen*; see Figure 2).

Motivators

Of 74 records, 49 discussed potential motivators. Many listed more than one motivator, bringing the total number of hypothesized motivators to 67. Table 2 contains motivators by order. Kin selection was the most frequently suggested motivator (20/67), followed by empathy (13/67).

Figure 2

Records Classified by Type of Research



Note. Rescue classifications by record number. True rescue was seen in Hymenoptera (n=13), Carnivora (n=4), Primates (n=4), Cetacea (n=4), and Other (n=5). Rescue adjacent was seen in Hymenoptera (n=9), Rodentia (n=4), Primates (n=1), and Other (n=1). Prosocial behavior was seen in Rodentia (n=16), and Carnivora (n=2).

Table 2

Hypothesized Drivers for Rescue/Rescue-Like Behavior by Order

Order	Driver	Number of Records
Hymenoptera	Kin Selection	10
	Colony defense/maintenance	5
	Antipredator defense	3
	Other	3
Rodentia	Empathy	12
	Prosocial behavior	4
	Emotional contagion/perception action model	4
	Other	3
	Kin selection	1
	Reciprocal altruism	1
Carnivora	Kin selection	4
	Empathy	1
	Emotional contagion/perception action model	1
Primates	Kin selection	4
	Reciprocal altruism	1
	Antipredator defense	1
	Other	1
Cetacea	Reciprocal altruism	2
	Kin selection	1
Other	Kin selection	2
	Reciprocal altruism	2
	Colony defense/maintenance	1
	Emotional contagion/perception action model	1

Discussion

The literature that is returned when using the search term "rescue behavior" focuses largely on two taxa, eusocial insects and rodents. Even though Nowbahari and Hollis (2010) created the term "rescue behavior" to be applied broadly across taxa and situations, it is currently applied narrowly, limiting the available literature. Our own definition, the Immediate Risk Rescue Criteria (IRRC), is applied even more narrowly, and thus reduced the number of articles returned further. We suggest two main reasons for this: many behaviors that could qualify as rescue under Nowbahari and Hollis' definition is discussed using different terms, and the "risk" component can be difficult to determine for both the rescuer and victim.

There are many behaviors than the ones we observed in this review that could be considered, or could become rescue behavior if the search terms were broadened slightly. For example, offspring defense by one or more individuals (Vogel & Fuentes-Jiménez, 2006), cooperative antipredator behavior (Shackleton et al., 2015), and mobbing could all be considered rescue (Crofoot, 2013). Additionally, despite the breadth of work on rescue behavior in eusocial insects, sanitary care, an allogrooming behavior related to social immunity in group-living insects, was not returned in this search despite meeting the requirements for rescue behavior. Rescue behavior, as it currently appears in the literature, seems to largely involve an adult rescuer coming to the aid of an adult victim, except for in a few cases (Cruz, 1986; Jack et al., 2020; Masilkova et al., 2021; Nowbahari et al., 2016; Vogel & Fuentes-Jimenez, 2006). This may be due in part to the fact that several terms regarding the defense of young were in use long before Nowbahari and Hollis discussed rescue behavior in 2010, such as "infanticide avoidance" (Hrdy, 1979), "maternal defense" (first coined as "maternal aggression" in 1968 by Moyer), and "nest defense" (Montgomerie & Weatherhead, 1988). So long as the defending adult is also at risk, defending offspring from a threat can often be considered rescue behavior.

There are many well-documented types of antipredator behaviors, where adults will specifically put themselves at higher risk of predation to protect the group's offspring. For example, large, group living herbivores such as African elephants (*Loxodonta africana*; Adams & Berg, 1980; Carrington, 1958) and American bison (*Bison bison*; Carbyn & Trottier, 1988) will create protective circles around the herd's young. These antipredator behaviors are well documented, particularly in nature documentaries, but published, peer-reviewed scientific literature of these particular behaviors is scarce. This protective circle phenomenon, even though it meets all of Nowbahari and Hollis' (2010) rescue criteria, was completely missed by this scoping review search. We suggest this phenomenon in particular was more likely missed by the "rescue behavior" literature search not because the search was too narrow, but because this behavior does not appear to have a clearly defined name, there are very few published articles, and the studies that do exist do not use the term rescue or altruism. In the case of nest/offspring/young defense (Ellison & Ribic, 2012; Liu et al., 2025), infanticide prevention (Agrell et al., 1998 Ebensperger, 1998), and maternal/parental defense (Estes & Estes, 1979), as well as the protective circling behavior, we argue that the search terms beyond rescue behavior better describe the behavior at hand.

Antipredator behavior can manifest in a variety of ways across taxa, and in group living animals is often a cooperative effort. While Nowbahari and Hollis (2010) do specifically discuss cooperative antipredator behavior, they note that it is: 1. Difficult to distinguish between an instance of rescue behavior and self-defense and 2. Possible for cooperative antipredator behavior to be rescue behavior, but that not all cooperative antipredator behavior is rescue. Nowbahari and Hollis note that because it is nearly impossible to determine if an individual is engaging in the rescue behavior or self-defense, interpreting antipredator behavior as rescue should be approached cautiously. We argue that one of the reasons why Nowbahari and Hollis' definition of rescue is so narrowly applied is due to this binary usage of the term rescue and the idea that risk must be all or none. Risk, both for the victim and the rescuer, is rarely all or none, and in most cases regarding any kind of altruistic behavior risk will occur on a continuum, resulting in a cost/benefit analysis prior to action.

In one widespread cooperative antipredator behavior, mobbing, individuals work together to approach and harass a threat (Carlson & Griesser, 2022). Mobbing behavior involves multiple risk assessments (Crofoot, 2012; Fang et al., 2020; Ostreiher, 2003), but to what extent the mobber is in danger

is likely dependent on many poorly understood factors (Carlson & Griesser, 2022). If the mobber is at risk by engaging in the mob, mobbing can quickly turn into rescue behavior if the threat has caught a victim (Eberle & Kappeler, 2008; Jack et al., 2020; Pitman et al., 2017, Rood, 1983). Rescue mobs are capable of drawing more mobbers than a predator without a victim (Carlson & Griesser, 2022).

Additionally, while behaviors like mobbing *may* be rescue behavior, they can also occur in the absence of a "true" threat or victim. In order for rescue behavior to occur, there must be an actual threat and a victim or an individual who will imminently become a victim. Antipredator behavior such as mobbing, fleeing, or defensive posturing often occurs when an animal perceives a threat, whether or not the threat is actual. For example, birds will mob artificial threats that bear only a passing resemblance to the actual predator (Bartmess-LeVasseur et al., 2010; Berankova et al., 2015; Book & Freeberg, 2015), or study skins clamped at a "lifelike" angle (Courter & Ritchison, 2010; Dahl & Ritchison, 2018). Plastic hawks, stuffed cats, paper-maché models, and study skins appear, to the human eye, significantly different from a live version. These stimuli pose no real danger, but are perceived as threats and elicit mobbing behavior. Because mobbing occurs so frequently without a victim present, and is frequently studied in contexts that do not allow the subject to be in any real danger, we suggest that like with the offspring defense terms, the term "mobbing" is more appropriate overall- even though this behavior could hypothetically fall under the rescue umbrella.

The majority of the existing literature on rescue behavior focuses on eusocial insects, particularly ants. Despite this, sanitary care, a well-documented behavior in ants, was not returned during this search. Sanitary care is a type of social immunity in which ants clean nestmates of pathogenic materials that threaten both the colony and the individual that carries them (Cremer et al., 2007). Fungal pathogens, in particular, threaten both the infected individual and the colony as a whole (Liu et al., 2019; Traniello et al., 2002). The cleaning ant acts as a rescuer in this case, removing pathogenic material from the cuticle of its nestmate. If the pathogenic material is not removed, then the infected individual's chance of survival decreases (Qiu et al., 2014). By removing the pathogen, the rescuer risks becoming infected as well (Cremer, 2019; though see Qiu et al., 2014). In our search, we found one paper that discussed a similar phenomenon in ants treating the wounds of injured nestmates (Frank et al., 2018).

We considered the paper by Frank and colleagues to be "true rescue," and so it stands that similar behaviors like the various strategies eusocial insects use to employ social immunity can also be considered rescue behavior. However, neither "social immunity" nor "sanitary care" were behaviors that appeared in our search. While we suggest that in part, the terms "social immunity" and "sanitary care" are more specific for these behaviors, we also suggest that there are anthropogenic biases in the way that the scientific literature describes similar behaviors. The overwhelming majority of the rescue and social release work on rodents is focused on whether empathy is the driving motivator of these release behaviors. However, the literature focused on eusocial insects does not discuss empathy as a motivator, instead focusing on kin selection and colony defense. This issue (i.e., invoking empathy as a motivator) is contentious in the context of rescue research and reflects the larger issue of anthropocentric biases in research more generally (Blystad, 2019, 2021; Hachiga et al., 2018; Schwartz et al., 2017; Silberberg et al., 2014).

Within the literature returned as "true rescue" in our search, the overwhelming majority of victims were in active danger, either captured by a predator/threat (17/30) or injured (7/30). The rest of the victims were in danger due to a reduction in resources (1/30), such fierce competition that they would starve (1/30), or were protecting their colony from being destroyed/eaten (4/30). Nowbahari and Hollis' (2010) definition states that the consequences of not being rescued must be physical but do not have to be direct- so we suggest that a victim that is not yet in danger but will be imminently should fulfill this requirement. Examples of this would include victims that are actively being targeted by a predator, such as a bison calf being singled out by wolves, or bear cubs that are being charged by an adult male. We suggest that even though these victims are in danger, because these examples involve some level of intentionality on the threat's behalf, they are not as common in the literature.

So then, what is rescue behavior? What behaviors are able to be classified as rescue? Should we even define rescue behavior separately beyond altruism and helping behavior? We suggest that while this scoping review on rescue only contains some of the behaviors that can be classified as rescue, it is not

necessarily only the result of an overly narrow definition on the part of Nowbahari and Hollis (2010). While mobbing, cooperative antipredator behavior, infanticide avoidance, and a host of other behavior may also sometimes qualify as rescue behavior, they are better described by other terms. Rescue behavior, or behavior that could be considered rescue behavior (e.g., offspring guarding behavior), may not be as rare as Nowbahari and Hollis suggest - but rather it is described and studied under other terms. We agree with Nowbahari and Hollis that the term "rescue behavior" should be defined separately beyond altruism and helping behavior. The term chosen for a mechanism of behavior is dependent in part on the species, for example: a rat may be motivated by "empathy" and ants may be motivated by "kin selection" instead. However, if both these behaviors are called "rescue behavior" then we can attempt to overcome anthropogenic biases in publication terms, and avoid semantic confusion. Future literature searches into the rescue behavior literature should use diverse search terms beyond altruism and rescue. We do suggest that because Nowbahari and Hollis are so strict on the "risk" component, it can create problems when trying to classify new behaviors as rescue.

When creating the terms under the IRRC, we made the term "true rescue" very narrow because determining the level of risk to a rescuer on such a broad scale is difficult. After conducting this literature review, we argue that due to the continuous nature of risk, and that risk can be so subjective, that the term "rescue behavior" can and should be used more loosely than Nowbahari and Hollis (2010) suggest. The individual rescuers may perceive the level of risk differently, for example, saving a drowning person is less dangerous for a trained lifeguard than an average bystander. Two researchers may also perceive a different level of risk when observing the same behaviors or interpreting the same data. The IRRC are strict criteria which can best be used when conducting a general literature search and review on rescue behavior following Nowbahari and Hollis' definition. This binary approach to risk is a weakness in both Nowbahari and Hollis' definition, and our own IRRC definition.

Despite the IRRC being so strict, we did find that some researchers test rescue when an individual helps another individual in distress or danger with no direct benefit to itself, instead of using Hollis and Nowbahari's (2010) four rescue criteria. Though we do note that many of these papers use the term rescue without operationally defining it (e.g., Cox and Reichel, 2020, 2021; Hachiga et al., 2018; Heslin & Brown, 2021; Quinn et al., 2018; Tomek et al., 2019, 2020; Silberberg et al., 2013; Silva et al., 2020; Ueno et al., 2019b). We suggest that using the shorter definition of rescue behavior is perfectly appropriate, so long as rescue itself is operationally defined in the context of the study. We note here that using a shorter definition can help expand the current literature on rescue behavior without sacrificing cases in which the costs and benefits of rescuing may be unclear, or exist on a continuum.

In conclusion, the literature on rescue behavior is diverse in both species and methods, though the literature is heavily biased towards ants and rats. Due to this diversity, we used qualitative methods to sort and classify the existing literature instead of performing true meta-analysis. We agree that Nowbahari and Hollis' (2010) definition of rescue can be a useful way to define and identify rescue behaviors across taxa, especially when the cost to a rescuer is immediately clear. The IRRC is extremely strict, but highlights the need for assessing risk in the context of rescue. While a key component to rescue, risk is a concept that is so subjective, and without better methods to assess risk in the context of rescue, behaviors that *could* be rescue are called something different, like mobbing or anti-predator behavior. Where there is enough literature on a specific species or using a specific methodology, theoretical models assessing risk to a rescuer could be developed. In the meantime, a broader definition of rescue is often more applicable than Nowbahari and Hollis' definition, or the IRRC.

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References

Adams, J., & Berg, J. K. (1980). Behavior of female African elephants (*Loxodonta africana*) in captivity. *Applied Animal Ethology, 6*(3), 257-276.45

Agrell, J., Wolff, J. O., & Ylönen, H. (1998). Counter-strategies to infanticide in mammals: costs and consequences. *Oikos*, 507-517.

Andras, J. P., Hollis, K. L., Carter, K. A., Couldwell, G., & Nowbahari, E. (2020). Analysis of ants' rescue behavior reveals heritable specialization for first responders. *Journal of Experimental Biology, 223*(5), jeb.212530.

Asadi, E., Khodagholi, F., Asadi, S., Kamsorkh, H. M., Kaveh, N., & Maleki, A. (2021). Quality of early-life maternal care predicts empathy-like behavior in adult male rats: Linking empathy to BDNF gene expression in associated brain regions. *Brain Research, 1767*, 147568.

Bartmess-LeVasseur, J., Branch, C. L., Browning, S. A., Owens, J. L., & Freeberg, T. M. (2010). Predator stimuli and calling behavior of Carolina chickadees (*Poecile carolinensis*), tufted titmice (*Baeolophus bicolor*), and white-breasted nuthatches (*Sitta carolinensis*). *Behavioral Ecology and Sociobiology, 64*, 1187-1198.

Ben-Ami Bartal, I., Decety, J., & Mason, P. (2011). Empathy and pro-social behavior in rats. *Science, 334*(6061), 1427–1430.

Ben-Ami Bartal, I., Rodgers, D. A., Bernardez Sarria, M. S., Decety, J., & Mason, P. (2014). Pro-social behavior in rats is modulated by social experience. *ELife, 3*, e01385.

Ben-Ami Bartal, I., Shan, H., Molasky, N. M. R., Murray, T. M., Williams, J. Z., Decety, J., & Mason, P. (2016). Anxiolytic treatment impairs helping behavior in rats. *Frontiers in Psychology, 7*, 195728.

Ben-Ami Bartal, I., Breton, J. M., Sheng, H., Long, K. L., Chen, S., Halliday, A., Kenney, J. W., Wheeler, A. L, Frankland, P., Shilyansky, C., Deisseroth, K., Keltner, D., & Kaufer, D. (2021). Neural correlates of ingroup bias for prosociality in rats. *Elife, 10*, e65582.

Beránková, J., Veselý, P., & Fuchs, R. (2015). The role of body size in predator recognition by untrained birds. *Behavioural processes, 120*, 128-134.

Blanchard, R. J., & Blanchard, D. C. (1971). Defensive reactions in the albino rat. *Learning and Motivation, 2*(4), 351-362.

Blanchard, R. J., Blanchard, D. C., Rodgers, J., & Weiss, S. M. (1990). The characterization and modelling of antipredator defensive behavior. *Neuroscience & Biobehavioral Reviews, 14*(4), 463-472.

Blight, O., Villalta, I., Cerdá, X., & Boulay, R. (2016). Personality traits are associated with colony productivity in the gypsy ant *Aphaenogaster senilis*. *Behavioral Ecology and Sociobiology, 70*(12), 2203–2209.

Blystad, M. H. (2019). A critical review of the rodent social release paradigm: empathy or socialreinforcement. *Revista Mexicana de Análisis de la Conducta, 45*(2), 199-222.

Blystad, M. H., Andersen, D., & Johansen, E. B. (2019). Female rats release a trapped cagemate following shaping of the door opening response: Opening latency when the restrainer was baited with food, was empty, or contained a cagemate. *PLOS ONE, 14*(10), e0223039.

Blystad, M. H. (2021). An opinion on the interpretation of social release in rats. *Biology Letters,17*(11), 20210355.

Book, D. L., & Freeberg, T. M. (2015). Titmouse calling and foraging are affected by head and body orientation of cat predator models and possible experience with real cats. *Animal Cognition, 18*, 1155-1164.Bramley, G. N., Waas, J. R., & Henderson, H. V. (2000). Responses of wild Norway rats (*Rattus norvegicus*) to predator odors. *Journal of Chemical Ecology, 26*, 705-719.

Carballo, F., Dzik, V., Freidin, E., Damián, J. P., Casanave, E. B., & Bentosela, M. (2020). Do dogs rescue their owners from a stressful situation? A behavioral and physiological assessment. *Animal Cognition, 23*(2), 389–403.

Carbyn, L. N., & Trottier, T. (1988). Descriptions of wolf attacks on bison calves in Wood Buffalo National Park. *Arctic, 41*(4), 297-302.

Carlson, N. V., & Griesser, M. (2022). Mobbing in animals: A thorough review and proposed future directions. *Advances in the Study of Behavior, 54*, 1-41.

Carrington, R. (1958). *Elephants*. Chatto and Windus: London.

Carter, G. G., Wilkinson, G. S., & Page, R. A. (2017). Food-sharing vampire bats are more nepotistic under conditions of perceived risk. *Behavioral Ecology, 28*(2), 565–569.

Carvalheiro, J., Seara-Cardoso, A., Mesquita, A. R., de Sousa, L., Oliveira, P., Summavielle, T., & Magalhães, A. (2019). Helping behavior in rats (*Rattus norvegicus*) when an escape alternative is present. *Journal of Comparative Psychology, 133*(4), 452–462.

Cassidy, K. A., & McIntyre, R. T. (2016). Do gray wolves (*Canis lupus*) support pack mates during aggressive inter-pack interactions? *Animal Cognition, 19*(5), 939–947.

Chapais, B., Girard, M., & Primi, G. (1991). Non-kin alliances, and the stability of matrilineal dominance relations in Japanese macaques. *Animal Behaviour, 41*(3), 481-491.

Connor, R., & Norris, K. (1982). Are dolphins reciprocal altruists? *The American Naturalist, 119(*3), 18.

Courter, J. R., & Ritchison, G. (2010). Alarm calls of tufted titmice convey information about predator size and threat. *Behavioral Ecology, 21*(5), 936-942.

Cox, S. S., & Reichel, C. M. (2020). Rats display empathic behavior independent of the opportunity for social interaction. *Neuropsychopharmacology, 45*(7), 1097–1104.

Cox, S. S. & Reichel, C. M., (2021). Current rodent models for the study of empathic processes. *Behavioural Pharmacology, 32*(2&3), 96-111.

Cox, S. S., Kearns, A. M., Woods, S. K., Brown, B. J., Brown, S. J., & Reichel, C. M. (2022). The role of the anterior insula during targeted helping behavior in male rats. *Scientific Reports, 12*(1), 3315.

Crampton, J., Frère, C., & Potvin, D. (2022). Australian Magpies *Gymnorhina tibicen* cooperate to remove tracking devices. *Australian Field Ornithology, 39*, 7–11.

Cremer, S. (2019). Social immunity in insects. *Current Biology*, *29*(11), R458-R463.

Cremer, S., Armitage, S. A., & Schmid-Hempel, P. (2007). Social immunity. *Current biology*, *17*(16), R693-R702.

Crofoot, M. C. (2013). Why mob? Reassessing the costs and benefits of primate predator harassment. *Folia Primatologica, 83*(3-6), 252-273.

Cruz, Y. P. (1986). The defender role of the precocious larvae of *Copidosomopsis tanytmemus Caltagirone* (Encyrtidae, Hymenoptera). *Journal of Experimental Zoology, 237*(3), 309-318.

Czechowski, W., Godzińska, E. J., & Kozłowski, M. (2002). Rescue behaviour 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. *In Annales Zoologici. Fundacja Natura Optima Dux. 52*(3), 423-431

Dahl, J. A., & Ritchison, G. (2018). Responses of Blue Jays (*Cyanocitta cristata*) to raptors that differ in predatory threat. *Avian Biology Research, 11*(3), 159-166.

Duhoo, T., Durand, J. L., Hollis, K. L., & Nowbahari, E. (2017). Organization of rescue behaviour sequences in ants, *Cataglyphis cursor*, reflects goal-directedness, plasticity and memory. *Behavioural Processes, 139*, 12–18.

Dzik, M. V., Carballo, F., Casanave, E., & Bentosela, M. (2021). Effects of oxytocin administration and the dog–owner bond on dogs' rescue behavior. *Animal Cognition, 24*(6), 1191–1204.

Ebensperger, L. A. (1998). Strategies and counterstrategies to infanticide in mammals. *Biological Reviews, 73*(3), 321-346.

Eberle, M., & Kappeler, P. M. (2008). Mutualism, reciprocity, or kin selection? Cooperative rescue of a conspecific from a boa in a nocturnal solitary forager the gray mouse lemur. *American Journal of Primatology, 70*(4), 410–414.

Ellison, K. S., & Ribic, C. (2012). Nest defense-Grassland bird responses to snakes. *Studies in Avian Biology, 43*, 149-159.

Elorriaga-Verplancken, F. R., & Acevedo-Whitehouse, K. (2017). Potential intersexual altruistic behavior in California sea lions (*Zalophus californianus*). *Aquatic Mammals, 43*(2), 208-213.

Estes, R. D., & Estes, R. K. (1979). The birth and survival of wildebeest calves. *Zeitschrift für Tierpsychologie, 50*(1), 45-95.

Fang, W. H., Hsu, Y. H., Lin, W. L., & Yen, S. C. (2020). The function of avian mobbing: an experimental test of 'attract the mightier' hypothesis. *Animal Behaviour, 170,* 229-233.

Foster, W. A. (1990). Experimental evidence for effective and altruistic colony defence against natural predators by soldiers of the gall-forming aphid *Pemphigus spyrothecae* (Hemiptera: Pemphigidae). *Behavioral Ecology and Sociobiology, 27*(6), 421-430.

Fraser, O. N., & Bugnyar, T. (2012). Reciprocity of agonistic support in ravens. *Animal Behaviour, 83*(1), 171-177.

Frank, E. T., Schmitt, T., Hovestadt, T., Mitesser, O., Stiegler, J., & Linsenmair, K. E. (2017). Saving the injured: Rescue behavior in the termite-hunting ant *Megaponera analis. Science Advances, 3*(4), e1602187.

Frank, E. T., & Linsenmair, K. E. (2017). Saving the injured: Evolution and mechanisms. *Communicative & Integrative Biology, 10*(5–6), e1356516.

Frank, E. T., Wehrhahn, M., & Linsenmair, K. E. (2018). Wound treatment and selective help in a termite-hunting ant. *Proceedings of the Royal Society B: Biological Sciences, 285*(1872), 20172457.

Hachiga, Y., Schwartz, L. P., Silberberg, A., Kearns, D. N., Gomez, M., & Slotnick, B. (2018). Does a rat free a trapped rat due to empathy or for sociality? *Journal of the Experimental Analysis of Behavior, 110*(2), 267-274.

Hammers, M., & Brouwer, L. (2017). Rescue behaviour in a social bird: Removal of sticky 'bird-catcher tree' seeds by group members. *Behaviour, 154*(4), 403–411.

Heslin, K. A., & Brown, M. F. (2021). No preference for prosocial helping behavior in rats with concurrent social interaction opportunities. *Learning & Behavior, 49*(4), 397-404.

Hiura, L. C., Tan, L., & Hackenberg, T. D. (2018). To free, or not to free: Social reinforcement effects in the social release paradigm with rats. *Behavioural Processes, 152*, 37-46.

Hollis, K. L., & Nowbahari, E. (2013a). A comparative analysis of precision rescue behaviour in sand-dwelling ants. *Animal Behaviour, 85*(3), 537–544.

Hollis, K. L., & Nowbahari, E. (2013b). Toward a behavioral ecology of rescue behavior. *Evolutionary Psychology, 11*(3), 147470491301100.

Hollis, K. L., Harrsch, F. A., & Nowbahari, E. (2015). Ants vs. antlions: An insect model for studying the role of learned and hard-wired behavior in coevolution. *Learning and Motivation, 50,* 68-82..

Hollis, K. L. (2017). Ants and antlions: The impact of ecology, coevolution and learning on an insect predator-prey relationship. *Behavioural Processes, 139*, 4–11.

Hollis, K. L., & Nowbahari, E. (2022). Cause, development, function, and evolution: Toward a behavioral ecology of rescue behavior in ants. *Learning & Behavior. 50*(3), 329-338.

Hrdy, S. B. (1979). Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology, 1*(1), 13-40.

Huang, J., Cheng, X., Zhang, S., Chang, L., Li, X., Liang, Z., & Gong, N. (2020). Having infants in the family group promotes altruistic behavior of marmoset monkeys. *Current Biology, 30*(20), 4047-4055.

Jack, K. M., Brown, M. R., Buehler, M. S., Cheves Hernadez, S., Ferrero Marín, N., Kulick, N. K., & Lieber, S. E. (2020). Cooperative rescue of a juvenile capuchin (*Cebus imitator*) from a Boa constrictor. *Scientific Reports, 10*(1), 16814.

Kalamari, A., Kentrop, J., Hinna Danesi, C., Graat, E. A. M., van IJzendoorn, M. H., Bakermans-Kranenburg, M. J., Joëls, M., & van der Veen, R. (2021). Complex housing, but not maternal deprivation affects motivation to liberate a trapped cage-mate in an operant rat task. *Frontiers in Behavioral Neuroscience, 15*, 698501.

Kandis, S., Ates, M., Kizildag, S., Camsari, G. B., Yuce, Z., Guvendi, G., Koc, B., Karakilic, A., Camsari, U. M., & Uysal, N. (2018). Acetaminophen (paracetamol) affects empathy-like behavior in rats: Dose-response relationship. *Pharmacology Biochemistry and Behavior, 175*, 146-151.

Kitano, K., Yamagishi, A., Horie, K., Nishimori, K., & Sato, N. (2022). Helping behavior in prairie voles: a model of empathy and the importance of oxytocin. *Iscience, 25*(4), 103991.

Koricheva, J., Gurevitch, J., & Mengersen, K. (Eds.). (2013). *Handbook of Meta-analysis in Ecology and Evolution*. Princeton University Press.

Kuczaj, S. A., Frick, E. E., Jones, B. L., Lea, J. S. E., Beecham, D., & Schnöller, F. (2015). Underwater observations of dolphin reactions to a distressed conspecific. *Learning & Behavior, 43*(3), 289–300.

Kurosu, U., Aoki, S., & Fukatsu, T. (2003). Self-sacrificing gall repair by aphid nymphs. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 270*(S1), S12-S14.

Kwapich, C. L., & Hölldobler, B. (2019). Destruction of Spiderwebs and Rescue of Ensnared Nestmates by a Granivorous Desert Ant (*Veromessor pergandei*). *The American Naturalist, 194*(3), 395–404.

Liu, L., Zhao, X. Y., Tang, Q. B., Lei, C. L., & Huang, Q. Y. (2019). The mechanisms of social immunity against fungal infections in eusocial insects. *Toxins*, *11*(5), 244.

Liu, Q., Yu, J., Lorrillière, R., Shen, C., Yin, D., Wan, D., Wei, L., & Wang, H. (2025). Effects of local nest predation risk on nest defence behaviour of Japanese tits. *Animal Behaviour, 219*, 123031.

Masilkova, M., Ježek, M., Silovský, V., Faltusová, M., Rohla, J., Kušta, T., & Burda, H. (2021). Observation of rescue behaviour in wild boar (*Sus scrofa*). *Scientific Reports, 11*(1), 16217.

Miler, K. (2016). Moribund ants do not call for help. *PLOS ONE, 11*(3), e0151925.

Miler, K., & Kuszewska, K. (2017). Secretions of mandibular glands are not involved in the elicitation of rescue behaviour in *Formica cinerea* ants. *Insectes Sociaux, 64*(2), 303–305.

Miler, K., Symonowicz, B., & Godzińska, E. J. (2017). Increased risk proneness or social withdrawal? The effects of shortened life expectancy on the expression of rescue behavior in workers of the ant *Formica cinerea* (Hymenoptera: Formicidae). *Journal of Insect Behavior, 30*(6), 632–644.

Miler, K., & Turza, F. (2021). "O Sister, where art thou?"—A review on rescue of imperiled individuals in ants. *Biology, 10*(11), 1079.

Miler, K., Yahya, B. E., & Czarnoleski, M. (2017). Pro-social behaviour of ants depends on their ecological niche—Rescue actions in species from tropical and temperate regions. *Behavioural Processes, 144*, 1–4.

Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G., & PRISMA Group*. (2009). Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *Annals of Internal Medicine, 151*(4), 264-269.

Montgomerie R. D., & Weatherhead P. J. (1988). Risks and rewards of nest defence by parent birds. *Quarterly Review of Biology, 63*, 167–187.

Moyer, K.E. (1968). Kinds of aggression and their physiological basis. *Communications in Behavioral Biology, 2*, 65-87

Nowbahari, E., Scohier, A., Durand, J.-L., & Hollis, K. L. (2009). Ants, *Cataglyphis cursor*, use precisely directed rescue behavior to free entrapped relatives. *PLoS ONE, 4*(8), e6573.

Nowbahari, E., & Hollis, K. L. (2010). Rescue behavior: Distinguishing between rescue, cooperation and other forms of altruistic behavior. *Communicative & Integrative Biology, 3*(2), 77–79.

Nowbahari, E., Hollis, K. L., & 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*(11), e48516.

Nowbahari, E., Amirault, C., & Hollis, K. L. (2016). Rescue of newborn ants by older *Cataglyphis cursor* adult workers. *Animal Cognition, 19*(3), 543–553.

Nowbahari, E., Hollis, K. L., Bey, M., Demora, L., & Durand, J.L. (2022). Rescue specialists in *Cataglyphis piliscapa* ants: The nature and development of ant first responders. *Learning & Behavior, 50*(1), 71–81.

Ostreiher, R. (2003). Is mobbing altruistic or selfish behaviour? *Animal Behaviour, 66*(1), 145-149.

Pallante, V., Stanyon, R., & Palagi, E. (2016). Agonistic support towards victims buffers aggression in geladas (*Theropithecus gelada*). *Behaviour, 153*(9-11), 1217-1243.

Perry, S., Manson, J. H., Dower, G., & Wikberg, E. (2003). White-Faced Capuchins cooperate to rescue a groupmate from a boa constrictor. *Folia Primatologica, 74*(2), 109–111.

Pitman, R. L., Deecke, V. B., Gabriele, C. M., Srinivasan, M., Black, N., Denkinger, J., Durban, J. W., Mathews, E. A., Matkin, D. R., Neilson, J. L., Schulman-Janiger, A., Shearwater, D., Stap, P., & Ternullo, R. (2017). Humpback whales interfering when mammal-eating killer whales attack other species: Mobbing behavior and interspecific altruism? *Marine Mammal Science, 33*(1), 7–58.

Qiu, H. L., Lu, L. H., Shi, Q. X., & He, Y. R. (2014). Fungus exposed *Solenopsis invicta* ants benefit from grooming. *Journal of insect behavior*, *27*(5), 678-691.

Quinn, L. K., Schuster, L. P., Aguilar-Rivera, M., Arnold, J., Ball, D., Gygi, E., Holt, J., Lee, D. J., Taufatofua, J., Wiles, J., & Chiba, A. A. (2018). When rats rescue robots. *Animal Behavior and Cognition, 5*(4), 368–379.

Rasa, O. A. E. (2010). A Case of Invalid Care in Wild Dwarf Mongooses. *Zeitschrift Für Tierpsychologie, 62*(3), 235–240.

Rood, J. P. (1983). Banded mongoose rescues pack member from eagle. *Animal Behaviour, 31*(4), 1261–1262.

Santos Junior, L. C., Silva, E. P., & Antonialli-Junior, W. F. (2021). Do *Odontomachus brunneus* nestmates request for help and are taken care of when caught? *Sociobiology, 68*(3), e6022.

Sato, N., Tan, L., Tate, K., & Okada, M. (2015). Rats demonstrate helping behavior toward a soaked conspecific. *Animal Cognition, 18*(5), 1039–1047.

Schino, G., & Aureli, F. (2009). Reciprocal altruism in primates: partner choice, cognition, and emotions. *Advances in the Study of Behavior, 39*, 45-69.

Schwartz, L. P., Silberberg, A., Casey, A. H., Kearns, D. N., & Slotnick, B. (2017). Does a rat release a soaked conspecific due to empathy? *Animal Cognition, 20*(2), 299-308.

Sen, A., Kara, A. Y., Koyu, A., Simsek, F., Kizildag, S., & Uysal, N. (2021). The effects of chronic restraint stress on empathy-like behaviour in rats. *Neuroscience Letters, 765*, 136255.

Shackleton, K., Al Toufailia, H., Balfour, N. J., Nascimento, F. S., Alves, D. A., & Ratnieks, F. L. W. (2015). Appetite for self-destruction: Suicidal biting as a nest defense strategy in Trigona stingless bees. *Behavioral Ecology and Sociobiology, 69*(2), 273–281.

Siebenaler, J. B., & Caldwell, D. K. (1956). Cooperation among adult dolphins. *Journal of Mammalogy, 37*(1), 126.

Silberberg, A., Allouch, C., Sandfort, S., Kearns, D., Karpel, H., & Slotnick, B. (2014). Desire for social contact, not empathy, may explain "rescue" behavior in rats. *Animal cognition, 17*(3), 609-618.

Silva, P. R., Silva, R. H., Lima, R. H., Meurer, Y. S., Ceppi, B., & Yamamoto, M. E. (2020). Are there multiple motivators for helping behavior in rats? *Frontiers in Psychology, 11*, 1795.

Stenstrom, K. H., Deimeke, M. J., Sahu, P. K., Smeltz, S. M. L., Sturdy, C. B. (2026). Risk vs. reward: A systematic review on the threat faced by mobbers. *Animal Behavior and Cognition*, *13*(2), 184-196.

Subhadeep, D., Srikumar, B. N., Rao, B. S., & Kutty, B. M. (2022). Ventral subicular lesion impairs pro-social empathy-like behavior in adult Wistar rats. *Neuroscience Letters, 776*, 136535.

Taylor, K., Visvader, A., Nowbahari, E., & Hollis, K. L. (2013). Precision rescue behavior in North American ants. *Evolutionary Psychology, 11*(3), 147470491301100.

Tofilski, A., Couvillon, M. J., Evison, S. E. F., Helanterä, H., Robinson, E. J. H., & Ratnieks, F. L. W. (2008). Preemptive defensive self-sacrifice by ant workers. *The American Naturalist, 172*(5), E239–E243.

Tomek, S. E., Stegmann, G. M., & Olive, M. F. (2019). Effects of heroin on rat prosocial behavior. *Addiction Biology, 24*(4), 676-684.

Tomek, S. E., Stegmann, G. M., Leyrer-Jackson, J. M., Piña, J., & Olive, M. F. (2020). Restoration of prosocial behavior in rats after heroin self-administration via chemogenetic activation of the anterior insular cortex. *Social Neuroscience, 15*(4), 408-419.

Traniello, J. F., Rosengaus, R. B., & Savoie, K. (2002). The development of immunity in a social insect: evidence for the group facilitation of disease resistance. *Proceedings of the National Academy of Sciences*, *99*(10), 6838-6842.

Turza, F., & Miler, K. (2022). Comparative analysis of experimental testing procedures for the elicitation of rescue actions in ants. *Current Zoology, 68*(2), 159–168.

Turza, F., Zuber, G., Bzoma, M., Prus, M., Filipiak, M., & Miler, K. (2020). Ants co-occurring with predatory antlions show unsuccessful rescue behavior towards captured nestmates. *Journal of Insect Behavior, 33*(1), 1–6.

Ueno, H., Suemitsu, S., Murakami, S., Kitamura, N., Wani, K., Matsumoto, Y., Okamoto, M., & Ishihara, T. (2019). Helping-like behaviour in mice towards conspecifics constrained inside tubes. *Scientific Reports, 9*(1), 5817.

Ueno, H., Suemitsu, S., Murakami, S., Kitamura, N., Wani, K., Takahashi, Y., Matsumoto, Y., Okamoto, M. and Ishihara, T. (2019). Rescue-like behaviour in mice is mediated by their interest in the restraint tool. *Scientific Reports, 9*(1), 1-10.

Uy, F. M. K., Adcock, J. D., Jeffries, S. F., & Pepere, E. (2019). Intercolony distance predicts the decision to rescue or attack conspecifics in weaver ants. *Insectes Sociaux, 66*(2), 185–192.

Vanderhooft, L., Tan, L., & Hackenberg, T. D. (2019). Demand for social contact in rats: Toward a quantitative analysis of social reinforcement value. *Revista Mexicana de Análisis de la Conducta, 45*(2), 330-358.

Vogel, E. R., & Fuentes-Jiménez, A. (2006). Rescue behavior in white-faced capuchin monkeys during an intergroup attack: Support for the infanticide avoidance hypothesis. *American Journal of Primatology, 68*(10), 1012–1016.

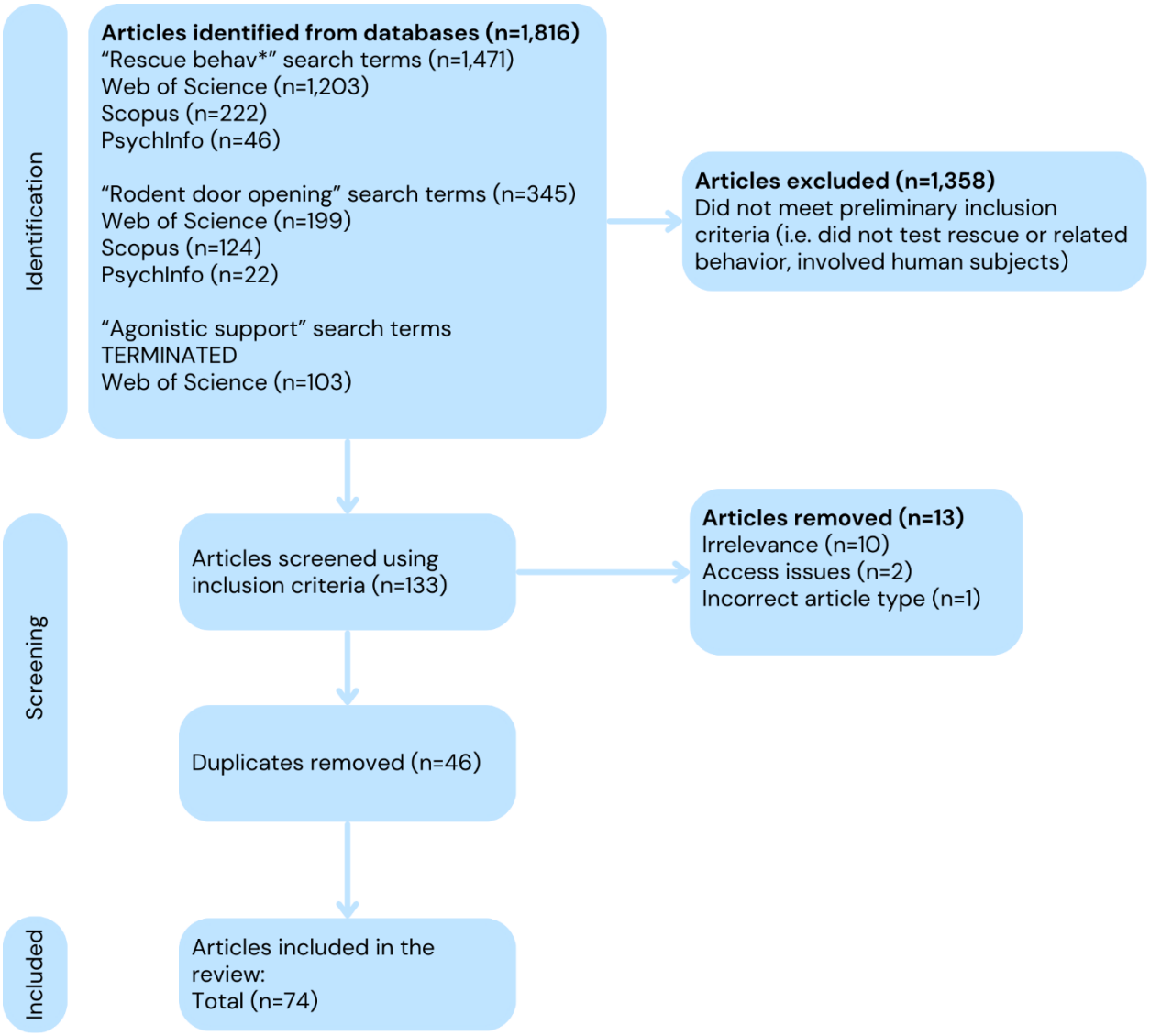
West, S. A., Griffin, A. S., & Gardner, A. (2007). Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, *20*(2), 415-432.

Yamagishi, A., Lee, J., & Sato, N. (2020). Oxytocin in the anterior cingulate cortex is involved in helping behaviour. *Behavioural Brain Research, 393*, 112790.

Yamagishi, A., Okada, M., Masuda, M., & Sato, N. (2020). Oxytocin administration modulates rats' helping behavior depending on social context. *Neuroscience Research, 153*, 56-61.

Supplementary Materials

Figure S1
PRISMA flow diagram detailing the search and inclusion process.



Note: This process included 74 articles in the final scoping review.