1

PROSOCIAL BEHAVIOR AND INTERINDIVIDUAL RECOGNITION IN ANTS

From Aggressive Colony Defense to Rescue Behavior

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Introduction

Ants, like many other eusocial insects—for example, honeybees, bumblebees, and termites—dominate their environment and adapt their behavior to it. Hölldobler and Wilson (2009) suggest that ants make up around 10% of extant insects worldwide and that ant colonies have been dominant elements of land habitats for at least 100 million years. The main reason for their ecological success is their sophisticated social organization, which is based on cooperation between members of two basic castes, namely a small reproductive caste and a much larger worker caste. The core of this social organization is reciprocal cooperative communication. A number of studies of social insects' behavior in different cooperative situations has shed light on the cognitive abilities required to accomplish these different tasks. However, prosocial behavior is often overlooked.

Prosocial behavior is defined as all social actions that benefit other members of the social group (Decety and Svetlova 2012) and has been investigated mainly in humans and other primates. Prosocial behavior includes altruistic behavior, which imposes the additional criterion that the behavior benefits the recipient but at a cost to the donor[1]. Altruistic behavior, at the first glance, would seem to defy Darwinian natural selection because it does not appear to benefit individual gene propagation. However, this evolutionary paradox is easily explained in terms of three principal theories: (1) The *kin selection theory* of Hamilton (1964) posits that the donors of altruistic acts obtain an indirect benefit whenever their behavior benefits close relatives, which of course are likely to share the donors' genes. Kin selection requires individuals to be able to recognize kin and non-kin. (2) Trivers' (1971) *theory of reciprocal altruism* posits that non-related individuals obtain a delayed benefit from performing altruistic acts if the social structure requires reciprocity. Reciprocal altruism requires individuals not only to recognize individuals but also to possess some form of scorekeeping memory mechanism that reduces the likelihood of cheating. Finally, (3) Zahavi's (1995) *prestige hypothesis* suggests that helping behavior is an honest signal, albeit a costly signal, of social prestige, a signal that is easily perceived by group members and that improves mating access or dominance status. Although Zahavi presented his prestige hypothesis as an alternative to kin selection, Lotem, Wagner and Balshine-Earn (1999) suggest that both theories may work together, with helping behavior evolving signals of individual quality. In short, then—and whether altruism derives from kin selection, reciprocal altruism or the search for prestige—it is an adaptive form of behavior and, thus, like other behavioral adaptations, is favored by natural selection.

Prosocial behavior exists in various forms and many taxa, from bacteria to primates. Recently, "altruistic-like" behavior has been demonstrated in bacteria. Many examples of antibiotic resistance, for example nosocomial (i.e., hospital-acquired) infections, have been known for many years but their mechanisms are not fully understood. However, in colibacillos infections with *Escherichia coli*, recent research has demonstrated that this resistance to antibiotics comes from a few (1%) very resistant bacteria that protect others by producing a molecule that makes them insensitive to the antibiotic. Because these super-resistant bacteria reproduce less quickly than others, their reaction to antibiotics constitutes a form of altruistic behavior that benefits individuals of the same clone at their own expense (Lee et al., 2010). Yeasts, too, also exhibit what might be called cooperation. For example, in *Saccharomyces cerevisiae* yeast, cells express a gene called FLO1 that triggers flocculation, a form of protection against stressors such as antibiotics or alcohol. These genes aggregate preferentially independently of the rest of the genome (Smukalla et al., 2008).

Eusocial ants, for example, demonstrate many different types of cooperation, including parental helping, reciprocal help, and a division of labor in which different groups of individuals specialize in particular tasks necessary to the colony as a whole. Prosocial behavior in ants also includes rescue behavior, an extreme form of altruistic behavior in which not only do ants place themselves in a risky situation to help a victim in a distress, but the rescuer is not rewarded and receives no benefit, except of course, the benefit that accrues from kin selection and reciprocal altruism (Nowbahari and Hollis, 2010). Yet another example of prosocial behavior in ants is aggressive colony defense, in which an ant places itself in a risky situation to protect its colony against intruders. These two latter forms of altruistic behavior, rescue and colony defense, display the remarkable cognitive capacities of ants—the capacity to distinguish nestmates from foreigners, the capacity to learn to recognize individual foragers, and the capacity to adapt their behavior accordingly.

In this chapter we focus on this ability of ants to adapt their behavior to these two very different social interactions. That is, in one of these types of social interactions, ants encounter potential intruders, and in the other they encounter distressed nestmates. Thus, in each encounter, an ant is in a specific situation that might be viewed as a decision point resulting in a series of behavioral patterns that demonstrate their sophisticated capacity for social recognition. The complexity and precision of these behavioral sequences are context-dependent and demonstrate the tendency of ants to accomplish a precise goal: either to scare off and eliminate the intruder or to release the nestmate from entrapment. We will show that these prosocial aptitudes are based on social cognition, which not only depends on phylogenetic membership but also changes during individual development (ontogenesis). We also present results demonstrating that chemical compounds are involved in these two situations, which act as signals to elicit the appropriate behavior.

Prosociality and Social Recognition

Social recognition is the basis of all social behavior and, from an evolutionary perspective, has fitness consequences for both the individual that performs the behavior and the recipient. The ability to discriminate between nestmates and foreigners has been observed in a large number of social hymenopteran species and particularly in ants (Breed and Bennette, 1987; Vander Meer and Morel, 1998; Lenoir et al., 1999; Breed et al., 2004). The underlying mechanisms of this discriminative ability to discriminate have been the object of much study. More than 90% of the signals used in these types of social communication by ants are chemical (e.g., Hölldobler and Wilson, 2009; d'Ettorre and Lenoir, 2010; Van Zweden and d'Ettorre 2010; Sturgis and Gordon, 2012). However, other signals, such as visual signals, sound and touch, also are used by many species in communication, but ordinarily just to amplify the effects of pheromones. Some signals are complex, combining smell, taste, vibration (sound) and touch. Notable examples are the waggle dance of honeybees, the recruitment trails of fire ants, and multimodal communication in weaver ants. To this list we can easily add colony defense and rescue behaviors in ants.

In the last four decades many studies have addressed the nature and location of production of the communication signals perceived by ants and other social insects (e.g., Bagnères and Morgan, 1991; Soroker et al., 1994; Sherman et al., 1997; Starks, 2004; Bos et al., 2010; Bos and d'Ettorre, 2012). Today, researchers acknowledge that ants and other social insects rely on chemical signals, particularly cuticular hydrocarbons (CHCs), which are a blend of long chain hydrocarbons present on the cuticle of each individual; because these CHCs are transferred from one or more of the several glands located in various parts of the ant's body, they constitute a signature mixture (Wyatt, 2010). Thus, ants are able to discriminate nestmates from non-nestmates using olfactory cues or contact chemoreception. Nestmates differ from non-nestmates by chemical cues produced by the individuals, which have a genetic basis, or in cues that are acquired from the environment, especially from their food (e.g., Crozier, 1987; Crosland, 1989a,b; Sorvari et al., 2008). This signature mixture serves as a template for comparing the encountered label with the internal representation of colony odor and hence determination of colonial membership; worker ants learn to recognize these cues early in adult life (Lenoir et al., 1999). Below we show how recognition of this colony label, in combination with additional chemical cues, or pheromones, that may be released from the same glands responsible for ants' CHCs, can evoke a variety of different responses, including aggressive colony defense, alarm or assembly response, recruitment, and rescue behavior.

Prosociality, Aggressive Behavior and Closure of Societies

Ants, like many social insects, normally attack conspecific intruders vigorously, even when intruders belong to the same species, which implies an accurate system of recognition. Colony existence often depends on the capacity of the colony to defend the nest, territory, and food sources against intruders (Stuart, 1988); indeed, colony defense maintains colony insularity against competitors and has played an important role in the evolution of eusociality (Wilson and Hölldobler, 2005). As Hermann and Blum (1981) reported, ants use a wide range of defensive mechanisms, including collective strategies and individual patterns of behavior. These behavior patterns, collectively called agonistic behavior (*sensu* De Vroey and Pasteels, 1978), appear to be distinctly aggressive (e.g., biting and stinging) and nonaggressive (e.g., escape and defensive immobility).

The animal behavior literature is full of examples of agonistic behavior in social interactions, especially predation and competition. Although at first glance agonistic behavior may not appear to be prosocial behavior, as a means of colony defense, it not only is a form of social cooperation, but also might be considered an especially extreme form of altruistic behavior because the defending individual places itself at great risk of injury while gaining no immediate benefit for itself. Nonetheless, because ant colonies typically consist of related individuals, defenders' receive an ultimate benefit via kin selection. Nestmate recognition acts as a proxy for kin recognition (Lenoir et al., 1999), allowing for social cohesion and protection of colony resources from competitors and parasites.

An example of the precision of non-nestmate recognition is shown in Figure 1.1, which shows the results of an experiment examining the diversity of aggressive reactions of resident ants toward a variety of intruder ants obtained from different colonies. The experiment was conducted with *Cataglyphis cursor*, a Mediterranean desert ant, whose colony size varies between 50 and 1600 individuals, The colony represents a *monogynous* society, meaning that it contains a single queen; moreover, *C. cursor* colonies are *parthenogenetic*, meaning that some individuals are asexually reproduced. Thus, not only are all individuals related to one another via a single mother, the queen, but also some individuals—those produced via asexual reproduction—are genetically identical. These monogynous

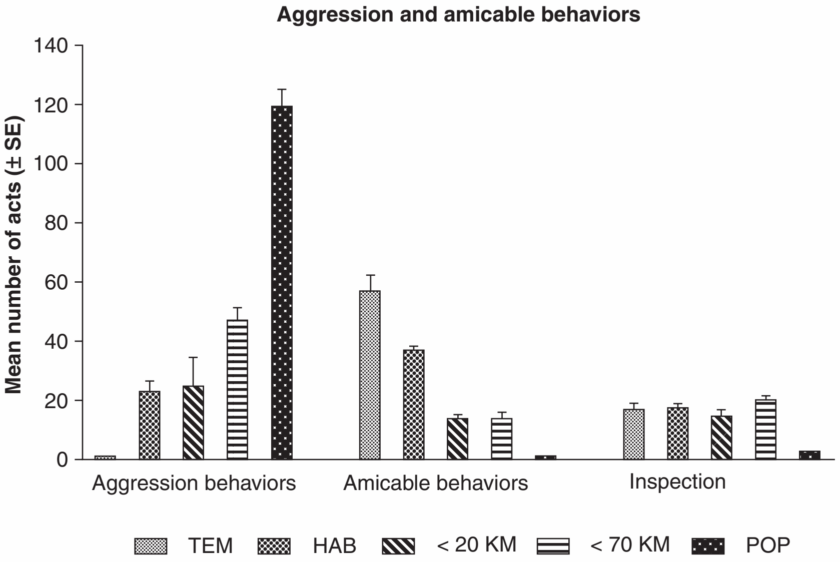

FIGURE 1.1 Mean number (± SE) of aggressive and "amicable" acts exhibited during a 15-min observation period by *Cataglyphis cursor* ants toward either a nestmate control (TEM) or a stranger ant from different habitats. HAB: Same habitat; < 20 Km: within 20 Km; > 70 Km: Habitat greater than 70 Km; POP: Habitat on opposite side of Rhone River.

and parthenogenetic characteristics of the colony would be expected to play a critical role in nestmate vs. non-nestmate recognition.

Each *C. cursor* colony was tested with four different kinds of stranger colonies: (a) the colony's close neighbors from the same habitat; (b) colonies from a different habitat less than 20 Km away; (c) colonies from an area more than 70 Km away; or (d) colonies collected in an area more than 70 Km away and separated by a natural barrier, namely the Rhone River. Because it cannot be crossed by ants, the Rhone essentially splits the ant population, producing two separate populations.

For each test an individually marked stranger ant was introduced in the foraging area of the resident colony. Then, during a 15-min observation period, all interactions with this stranger, in the foraging area or inside the nest, were recorded. Lastly, 72 hours later the colony was inspected to determine whether the stranger ant was adopted or rejected.

The results show a clear link between levels of aggression, recognition and geographical distance from the test colony and the possibility of adoption. Aggressive behavior was more intense when it was directed toward ants that came from geographically distant colonies and less intense when it was directed toward intruders from colonies of the same habitat (Figure 1.1). Concerning the adoption or rejection of foreign ants, when intruders originated from colonies within the same habitat, approximately 64% of ants were adopted. This result was not surprising because the colony reproduces by *fission*, meaning that a new colony is formed by a group of emigrant workers from the original colony together with another emigrant that has the potential to become their new queen (Lenoir et al., 1990); thus, colonies within the same habitat are likely to be relatives. When, however, intruders were from colonies in a different habitat, the adoption rate was significantly less, namely 42% (<20 Km) and 38% (>70 Km), respectively. Finally, in the case of very distant colonies separated from one another by the Rhone River, considered as two populations, intruders were vigorously attacked and killed (Nowbahari and Lenoir, 1984).

A detailed analysis of the different aggressive or defensive agonistic reactions elicited by intruders either inside the nest or in the foraging area clearly shows that the social environment has an important influence on the ability of ants to discriminate between nestmate and stranger cues (Figure 1.2). Inside the nest, the presence of so many nestmates leads to an increase in recognized odors and, thus, strangers are subject to less aggressive reactions particularly when they come from neighboring colonies in the same habitat. A comparison of CHCs obtained from ants found in different locations and quantified using gas chromatography verified that the ant populations are genetically different on each side of the Rhone River; indeed, at least two subspecies have been identified (Figure 1.2).

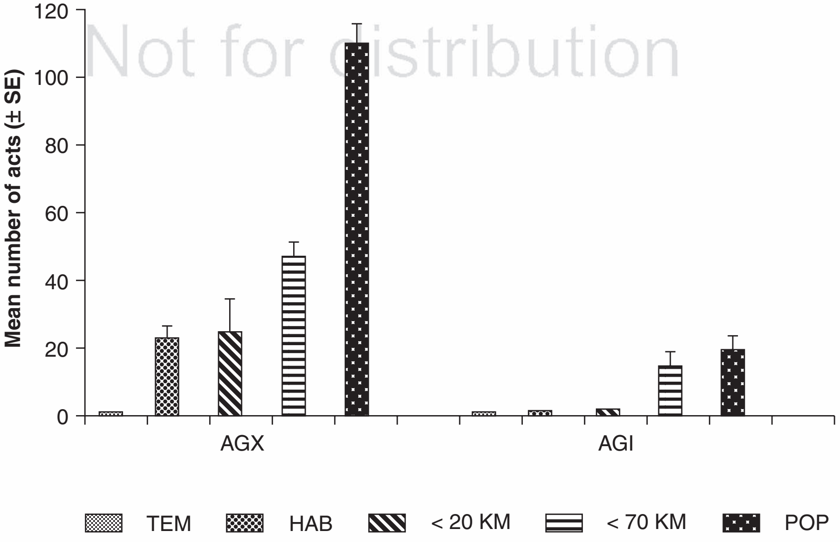

FIGURE 1.2 Mean number (± SE) of aggressive acts exhibited during a 15-min observation period by *Cataglyphis ants* toward either a nestmate control (TEM) or a stranger ant from different habitats either outside the nest (AGX) or inside the nest (AGI). HAB: Same habitat; < 20 Km: within 20 Km; > 70 Km: Habitat greater than 70 Km; POP: Habitat on opposite side of Rhone River.

Finally, further CHC analysis also shows that colony recognition, as indicated by aggressive behavior and adoption of a foreign ant, is highly correlated with CHC composition (Nowbahari et al., 1990).

Aggressive Behavior: Factors Influencing Inter-Individual Variation in Behavior

Many studies have shown especially striking variation between individuals' activity levels in both ant colonies and in bee hives (DeVroey and Pasteels, 1978; Breed, 1998; Hölldobler and Wilson, 2009). Some individuals are described as "hyperactive" while others are considered "lazy." For example, when the colony is moving, most of the transport is undertaken by only a few hyperactive ants in *Tapinoma sp* (Meudec 1979). In *Temnothorax rugatulus*, an ant species found in higher elevation coniferous forests, many individuals are remarkably lazy, remaining completely inactive during periods of especially high activity levels, which occur typically in late morning and again in late afternoon (Charbonneau et al., 2015).

C. cursor ant societies, which accept foreign individuals, exhibit much individual variation in activity levels, including worker aggression. Several factors influence this variation in workers, including their age; their particular behavioral function—their *division of labor* or *caste*—in the colony, for example whether they are nurses or foragers; and their *size polymorphism*, namely the degree to which different castes of workers exhibit different sizes and body types or *morphs*.

In experiments in which foreign ants from different colonies of *C. cursor* were introduced, ants exhibited pronounced individual behavioral differences, especially in the expression of aggression. Size played a critical role: Based on measurements of 253 stranger workers, consisting of small, medium and large ants, 60% of small individuals were adopted compared to only 44% of large ants; roughly half of medium-sized intruders were adopted (Nowbahari, unpublished data).

The degree of aggressive behavior toward intruders also depends on their polyethism or the division of labor. In insect societies, the influence of age on division of labor is well known. *C. cursor* exhibits *temporal polyethism* in which foragers—typically the oldest members of the colony—are responsible for foraging, whereas nurses specialize in brood care, and inactives, the youngest workers, remain near the brood but almost never tend to react toward strangers (Retana and Cerdá, 1990). The analysis of resident ants' reactions towards the introduction of individual foreign ants showed that foreign nurses were exposed to less aggressive behavior and were significantly more likely to be adopted than foreign foragers (Nowbahari, 1988).

To verify the existence of a functional group or sub-caste in colonial recognition, each of two groups of five ants, either nurses or foragers, were collected from colonies of different populations and were placed together in a circular box 6 cm in diameter. Three variants of the experiment were carried out: foragers were placed with foragers; nurses were placed with nurses; foragers were mixed with nurses. In each case, all aggressive behavior was recorded after the first 30 min, then 24h, 48h, and 72h later. The results showed that the foragers were very aggressive toward strangers that came from distant colonies. When two groups of five foragers were placed together, typically 70% were killed. When, however, a group of foragers was placed with a group of nurses, or when nurses were placed with nurses, aggressive behavior was significantly more limited than the forager-forager interactions. In sum, these results confirm a relation between temporal polyethism and degree of aggressiveness (Nowbahari, 1988).

Ontogenesis of Aggressive Behavior in Ants, *C. cursor*: A Representation of Nestmate Identity

In social insects, *callows*, recently hatched worker ants, are generally adopted by foreign colonies, even by those colonies that are totally closed to adult ants, for example, the *C. cursor* colonies located on either side of the Rhone River used in experiments described above. This acceptance of callows is the result of negligible levels of recognition signals, what Lenoir et al. (1999) call "chemical insignificance."

A series of experiments (Nowbahari & Lenoir, 1989) determined the age at which workers are recognized as foreigners by another colony. Newly hatched ants (0–8 hours old) and young ants of different ages (1–4 days old) were introduced into a distant colony. The transfer was performed on eight colonies located on two sides of the Rhone River. Finally, when a callow was adopted and integrated in the colony, they later were reintroduced into their original colony. In parallel with observations of ants' reactions to introduced foreigners, the CHC profile of the adopted callows was compared to the CHC produced by adult resident and foreign colonies.

The results show progressive and significant changes in the reactions of resident ants, depending on the age of the young workers and the consequent modifications to their odor profile over the first four days of their life (Figure 1.3). This period may represent a sensitive period for the establishment of the individual's odor and is a very important period for the individual's life (Nowbahari and Lenoir, 1988). These results are some of the first data obtained in ants identifying this sensitive period of development of individual odor, a sort of identity cue. In addition, and contrary to results with adult ants, newly hatched ants are frequently but not invariably adopted in a foreign colony. Perhaps even more surprising, the CHC of adopted callows is intermediate between the CHC profiles of the mother colony and the adoptive colony (Nowbahari et al., 1990). These adopted callows were able to live in either their original or their adopted colony, even though the adults of these colonies do not tolerate one another.

These results are similar to several studies of slave maker species. For example, in *Formica gagates* or in *Formica cunicularia*, slave ants are stolen as cocoons and emerge in the host colony where they behave toward their hosts as colony

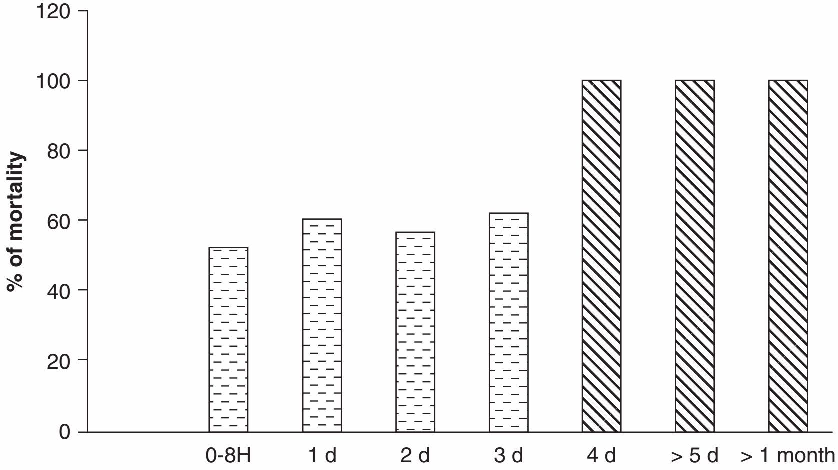

FIGURE 1.3 Percent mortality experienced by stranger *Cataglphis cursor* callows as a function of the age of the callow test stimulus. H = hour; d = day.

members (Lenoir et al., 2001). Similarly, in another slave maker species, *Polyergus rufescens*, slave-maker queens are tolerated by adult host workers, probably because they do not bear a specific CHC but instead attempt to mask themselves with substances from their hosts (d'Ettorre and Heinze, 2001).

Pro-sociality and Rescue Behavior: An Extreme Form of Altruistic Behavior

Rescue behavior, yet another extreme form of altruistic behavior because the rescuer risks injury or death, is a fascinating example of animals' cognitive capacity to detect and respond to another individual's distress—some might say to *empathize* with another individual—and as such, is often understood as a uniquely human response. Nonetheless, some of the earliest, often cited, examples of rescue behavior in the scientific literature are observational reports of dolphins assisting injured pod members by lifting them to the surface to breathe (Siebenaler and Caldwell, 1956). Similarly, dolphins also have been observed attempting to rescue companions by pulling on fishermen's nets in which the victims were trapped, or by biting the lines of harpoons (Caldwell and Caldwell, 1956). Another example of mammalian rescue behavior is the report of a male capuchin monkey helping a mother-infant pair escape a group of foreign attackers (Vogel and Fuentes-Jiménez, 2006). Finally, Bartal et al. (2011) reported that rats were able to learn to open a door to free a trapped cagemate in distress. On the basis of these experiments, Bartal et al. (2011) suggest that rats not only display prosocial behavior to eliminate distress in another, even without concrete reward, and argue that the rescuer's behavior is an empathically motivated behavior. This interpretation has been refuted by Siberberg et al. (2014), who demonstrate that the same behavior can be explained by rats' pursuit of social contact, and a recent work (Sato et al., 2015) has challenged this simple interpretation, arguing for "empathy-like" feelings in rats.

Whether one accepts the empathy interpretation of rats' behavior or not, rescue behavior in ants presents an interesting scientific challenge. The question is now on the possibility of empathy in insects. Recent research showed that *Drosophila* exhibits component behaviors of the fear response, suggesting the presence of emotion primitive behaviors. Hungry *Drosophila* flies were placed in a chamber with food and an automated fan blade was used to create a temporary shadow over the chamber. In response, the flies were distracted from eating and deserted the food source, even after the final shadow passed, demonstrating the emotion primitives of context generalization and persistence. As the shadow appeared with increasing frequency, the flies ran away more quickly, suggesting that their fear response is scalable, as well. It is not just a robotic reflex; there is some sort of internal state that develops (Gibson et al. 2015).

Anecdotes of rescue behavior in ants were reported as early as 1874 (Belt, 1874). Later, researchers described ants' ability to pull on the limbs of, and dig the sand away from, entrapped victims (Lafleur, 1940; Wilson, 1958; Markl, 1965; Blum and Warter, 1966; Spangler, 1968; Hangartner, 1969). More recently, a team of Polish researchers (Czechowski et al., 2002) described the ability of *Formica* ants to rescue a nestmate trapped in the pit of an antlion, a common predator of ants, by digging the sand and pulling the nestmate's limbs. Although none of these previous studies explored rescue behavior experimentally, more recent work, both in the laboratory and in the field, has begun to establish an ecological profile of rescue behavior in ants (Nowbahari et al., 2009; Hollis and Nowbahari, 2013; Taylor et al., 2013).

Precision Rescue Behavior in Ants, *Cataglyphis cursor*: A Laboratory Experiment

In one experiment (Nowbahari et al., 2009), a natural distress situation was simulated by binding a *C. cursor* worker to a small piece of filter paper with nylon thread and placing it in a small arena with a group of potential rescuers near the rescuers' nest entrance. Victims were either (1) a nestmate (homocolonial test); (2) a conspecific (heterocolonial test); (3) a stranger ant from a different ant species (heterospecific test); (4) a common prey item; or one of two controls, namely (5) a nestmate anesthetized by chilling or (6) an empty snare apparatus.

The results of this experiment revealed that only active nestmates (homocolonial test) evoked any form of rescue behavior. Rescue behavior never was observed in any of the remaining tests, i.e., heterocolonial ants, heterospecific ants, prey stimuli, ensnared motionless (anesthetized) nestmates, or the empty snare apparatus (Figures 1.4 and 1.5). These results are the first experimental evidence

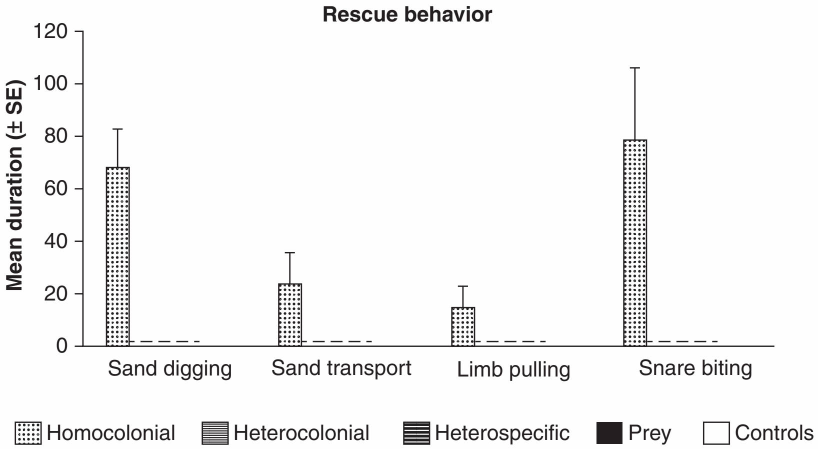

FIGURE 1.4 Mean duration (± SE) of four rescue behavior patterns (sand digging, limb pulling, snare biting and sand transport) performed by groups of five *Cataglyphis cursor* ants in response to a test stimulus, which was either a nestmate (homocolonial), a member of another colony of *C. cursor* (heterocolonial), a member of another ant species (heterospecific); a prey item; or a control test stimulus, either an ensnared but anesthetized nestmate or an empty filter-paper-and-snare apparatus.

Note: Adapted with permission from Nowbahari et al. (2009).

of rescue behavior in ants, demonstrating that *C. cursor* ants are able to recognize a nestmate in distress and to direct their responses to free only entrapped nestmate victims. That is, when *C. cursor* ants were presented with an experimentally bound nestmate victim, rescuers not only engaged in sand digging and limb pulling, both of which are forms of rescue behavior previously described in ants (e.g., Lafleur, 1940; Wilson, 1958; Markl, 1965; Spangler, 1968; Hangartner, 1969), but also when digging and pulling did not result in the victim's release, ant rescuers next transported particles of sand away from the victim's body, and, most importantly, bit specifically at the nylon snare that entrapped the nestmate. Somehow, ant rescuers were able to detect what, exactly, held victims in place: they exposed the nylon thread, and then immediately bit and tugged at the snare directly. As proposed by Nowbahari and Hollis (2010), *C. cursor* ant rescuers are capable of engaging in a precisely directed form of prosocial behavior that is different from cooperation, helping or other simple forms of altruistic behavior. That is, rescue necessarily consists of four components: (1) The victim is in a distress situation or in danger; (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, beyond, of course, the ultimate benefit to the rescuer's *inclusive fitness*.

FIGURE 1.5 Photograph illustrating precision rescue behavior in *Cataglyphis cursor* ants. A forager rescuer (center) is shown biting the nylon thread snare that holds the forager victim (right) to the paper filter. The rescuer already has transported sufficient sand away from the victim, exposing the white filter paper as well as the nylon thread snare holding its nestmate in place.

Note: Individuals were marked for identification purposes. Photograph by Paul Devienne. Adapted from Nowbahari et al., 2012.

A Comparative Analysis of Rescue Behavior

To determine how common is the phenomenon of precisely directed rescue behavior in ants, and to test whether rescue occurs only between close relatives, the laboratory experiment described in the previous section was adapted for the field and used to examine additional Mediterranean ant species (Hollis and Nowbahari, 2013) and two North American species (Taylor et al., 2013).

The results of these experiments revealed that two species, *Cataglyphis floricola*, a close relative of *C. cursor*, and *Lasius grandis*, another sand-dwelling species, both exhibited extremely high levels of rescue behavior, not only performing exactly the same four behavior patterns as did *C. cursor* in the previous laboratory experiment, but also restricting their aid to homocolonial nestmates (Figure 1.6). These two species not only inhabit a similar habitat as *C. cursor*, namely fine, easily disturbed sandy soils—soils also occupied by a common predator, pit-trapping larval antlions—but also they forage individually. In contrast, two other species, both belonging to the genus, *Messor*, rarely exhibited any form of rescue behavior. These *Messor* species live in habitats very different than *Catglyphis* or *Lasius*

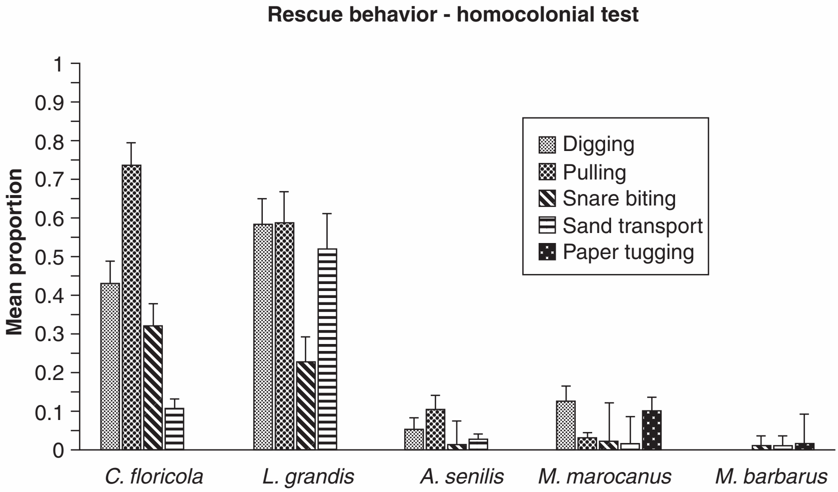

FIGURE 1.6 Mean proportion (± SE) of intervals in which ants exhibited rescue behavior (sand digging, limb pulling, snare biting and sand transport) or non rescue behavior (paper tugging) in response to a homocolonial nestmate. Five species of sand-dwelling Mediterranean ants were tested separately: *Cataglyphis floricola*, *Lasius grandis*, *Aphaenogaster senilis*, *Messor marocanus* and *Messor barbarus*.

Note: Adapted with permission from Hollis and Nowbahari (2013).

ant species, where the soil is very compact, and not at all easily collapsible and nowhere near the pits of predatory antlions. In addition, these two species forage collectively and form long, marked trails to food (López et al., 1993; Hölldobler and Wilson, 2009). Thus, the opportunity to become trapped and in need of rescue, either in its nest or en route to food, would be virtually nonexistent. Although *M. marocanus* did exhibit some digging behavior, this activity was far from rescue: When ants uncovered the victim attached to the filter paper by digging, they pulled it away from the nest to where they store other detritus, and then they ignored the victim for the rest of the test.

Concerning *Aphaenogaster senilis* ants, their behavior was puzzling. This ant exhibited each of the four rescue behavior patterns on a few occasions; but rescue was rare or nonexistent in most of test trials. The behavior of these ants may suggest that rescue behavior developed in a very distant ancestor of extant species but has been maintained only in some species for which rescue could play a critical role in its fitness. This hypothesis awaits further testing in *basal* species, namely those close to the root of the phylogenetic tree. Nonetheless, some initial data indicate that, as hypothesized, even ants belonging to basal species are able to recognize their nestmates and are capable of performing rudimentary forms of each of the behavior patterns observed in rescue behavior. However, only those species that live in the same sandy habitat where there is some risk of entrapment by collapsing sand and predatory antlions accomplish the highly complex, precisely directed rescue behavior.

Finally, research with two North American ant species, namely *Tetramorium sp. E* and *Prenolepis impairis*, confirmed the important roles of habitat and relatedness in rescue behavior (Taylor et al., 2013). *T. sp. E* forage individually and, very much unlike *P. impairis*, their nests are located close to antlion pits. As Figure 1.7 illustrates, *T. sp. E*, but not *P. impairis*, engaged in rescue behavior. Unlike the results with *Cataglyphis* and *Lasius* ant species, however, *T. sp. E* also rescued heterocolonial ants, that is, ants belonging to a different colony. Although this behavior may at first appear like a failure of nestmate recognition, *T. sp. E* are thought to be unicolonial (Steiner et al., 2003), forming especially large societies that can include hundreds of nests between which workers and queens can move freely without aggression (Helanterä et al., 2009). Thus, the rescue of heterocolonial victims actually involved relatives.

The rescue tactics of *Tetramorium* are especially interesting in that these ants adapted their rescue behavior to the object that entrapped the victim: When offered the opportunity to rescue a nestmate from an actual antlion pit, *Tetramorium* rescuers pulled on the limbs of nestmates held by a live predatory antlion and transported sand away from nestmates that had been pulled under the sand by the antlion (Figure 1.7). In addition, when the victim was bound to a piece of filter paper by a snare, the rescuer bit the snare but when, instead, the victim had

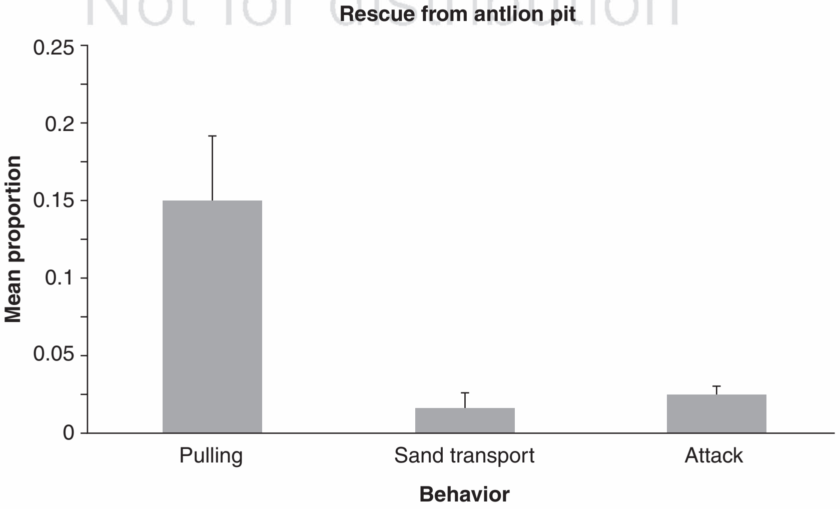

FIGURE 1.7 Mean proportion (± SE) of intervals in which *Tetramorium sp. E* rescuers engaged in each of three rescue behavior patterns, namely limb pulling, sand transport or antlion attack, in response to a nestmate captured by an antlion.

Note: Adapted with permission from Taylor et al., 2013.

been captured by an antlion, the rescuer bit the antlion, attempted to dismember it by pulling on its mandibles and used its stinger to deliver formic acid (Taylor et al., 2013).

In sum, studies of rescue behavior in multiple species of ants suggest that ecological factors may play a pivotal role in determining which species engage in rescue behavior and which do not. This form of prosocial behavior, in which individuals respond to another individual in distress, may be far more widespread and shared among animal species than one might expect. Indeed, unless one can accept that ants, too, are capable of recognizing distress in another individual and seeking the means to alleviate that distress—what some have called "empathy-like behavior" (Sato et al., 2015)—ant rescue provides scientists with several explanatory challenges: What are the necessary and sufficient conditions for "recognizing" distress in another? What kinds of proximate mechanisms—and how many different mechanisms—operating in very different animals, from ants to primates, might enable them to detect distress and respond appropriately? And, finally, how might we distinguish between mechanisms that appear to produce the same precisely directed, goal-motivated behavior (Vasconcelos et al., 2012)?

Age-Related Changes in Rescue Behavior and Social Recognition

Division of labor, an adaptation in which individuals engage in distinct functions such as brood-care, defense or foraging, largely contributes to the ecological success of insect society (Hölldobler and Wilson, 1990; Beshers and Fewell, 2001). Morphological, genotypic, or age variation (temporal polyethism) are different forms of division of labor. According to Retana and Cerdá (1991), mentioned above, division of labor in *C. cursor* ants is based on *temporal* or *age polyethism* where workers labor in the nest when they are young and forage or defend the nest outside when they are older. Therefore, during each behavioral phase, a worker may belong to a particular age caste for a sustained period of time. Younger workers, called inactives, initially do not participate in colony tasks but, then perform tasks inside the colony as nurses and then, when they become older, they labor outside the nest by foraging or nest colony defense (Robinson, 1992).

Throughout all the experiments examining rescue behavior, either in the laboratory or in the field, it was clear that not all adult workers are capable of administering help and not all endangered ants are capable of eliciting help. Subsequent research with *C. cursor* has revealed that rescue behavior is controlled by a division of labor widespread in social insects.

In those experiments, groups of five potential rescuers of the same caste obtained from the same colony—either five foragers, five nurses, or five inactives—and each were paired with an experimentally ensnared ant victim—either an inactive, a nurse, or a forager. The results, which are presented in Figure 1.8, reveal that caste membership determines not only the ability to provide aid, but also to

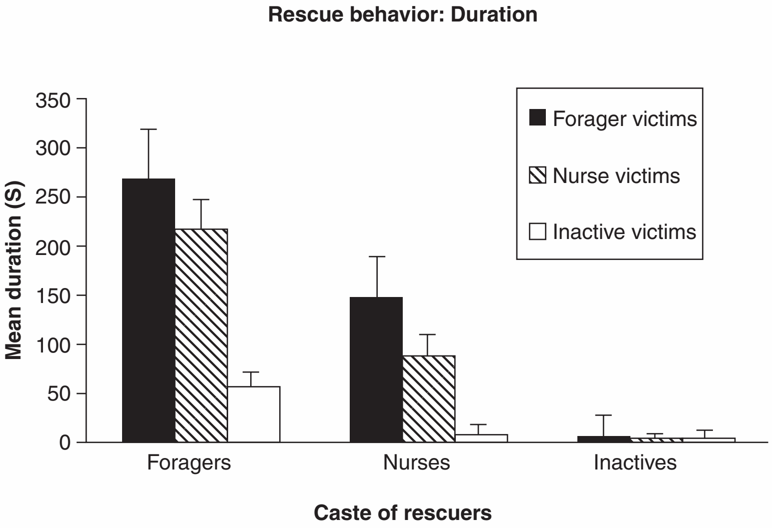

FIGURE 1.8 Mean duration (± SE) of nestmate rescue behavior performed by a group of five *C. cursor* rescuers from different castes, either all foragers, all nurses or all inactives, in the presence of a single experimentally ensnared victim, either a forager, a nurse or an inactive.

receive it. Specifically, foragers were able both to administer and to obtain the most help whereas inactives, the youngest individuals, were incapable of providing help to victims, as well as eliciting help from potential rescuers, regardless of their caste. Nurses generally performed intermediate levels of aide, reflecting their intermediate age status. These data thus reveal a novel behavioral specialization based on age-polyethism in eusocial insects, namely rescue behavior. Indeed, the occurrence and intensity of this behavior in each caste reflects exactly the same temporal polyethism pattern already observed for executing other tasks performed by colony members (Retana and Cerdá, 1990).

Insights from developmental biology may be useful in understanding the participation of different caste members in rescue behavior. In ants, as other social insects, the division of labor, and especially temporal polyethism in which workers' activities change systematically during their development, illustrates physiological maturation of the brain, as has been demonstrated in another *Cataglyphis* species, *C. albican* (Seid and Wehner, 2009), as well as glandular development (Robinson, 1992). For example, in *Myrmica rubra* worker ants, secretions produced by Dufour and poison glands, which are used to signal alarm (Cammaerts-Tricot in 1974), increase with age. Recently, in a study of *C. cursor* pheromones, we found some evidence that these same two glands are involved in rescue behavior (unpublished data). Thus, we suggest that, because *C. cursor* foragers are the oldest workers, they almost certainly possess a more developed nervous system and have more well-developed glands than either nurses or inactives, which enable foragers not only to recognize the call-for-help signal of nestmate victims but also to emit a more intense alarm signal of their own when they require help. In turn, nurses would be expected to give and receive help more than the less-developed inactives.

These caste specific differences in rescue behavior represent a highly adaptive specialization for rescue that is finely tuned to a caste member's probability of becoming, or encountering, a victim in need of rescue: Like foragers in all insect societies, *C. cursor* foragers are the only colony members to travel far away from the nest. Thus, they are the only individuals that risk becoming trapped as they search for and retrieve food, whereas nest-bound inactives would be unable to provide aid to distant foragers. Finally, nurses, specialized for brood care, likely possess some of the same behavioral patterns shown by efficient forager rescuers.

Conclusions

Social cognition is the key mechanism of social organization and cohesion in social insects. In ants, as other eusocial insects, all colony members are relatives (Lenoir et al., 1999) and they have evolved a highly developed recognition system enabling them to collaborate and to behave altruistically toward nestmates, but to react aggressively toward intruders. Ants' communication system is based on chemical cues, including the ability to discriminate relatives from strangers and to adjust a reaction to a particular situation, namely to perform an aggressive response when defending the colony, or to perform rescue behavior when encountering a nestmate in distress.

Aggressive defense, the outcome of recognizing a foreigner, has been observed and described in nearly all invertebrate groups. In many cases, the presence or absence of aggression, as well as the intensity of its expression, is known to vary with time and environmental conditions. Such variation in invertebrates suggests the operation of the individual's capacity to discriminate between chemical signals. Studies in several social insect species suggest that this capacity could also change according to the individual's maturation, that is, during its development or ontogenesis, as well as geographic distance between colony origin, caste and morphologic size, all of which is reflected in ants' CHCs (Nowbahari et al., 1990).

Experiments with newly hatched individuals, callows, permit a better understanding of the acquisition of individual cues and the importance of sensitive period in *C. cursor* ants (Nowbahari and Lenoir, 1988). Although callows lack recognition chemical cues on their body surface (Lenoir et al., 1999), they are recognized as nestmates, simply because they are present in nest. Because they lack CHCs, they can be transferred from one nest to other without being attacked. Nonetheless, the experiments with callows demonstrate the existence of a sensitive period in which they acquire a chemical cue identity reflecting their social environment. That is, when callows were introduced to a foreign colony during the four first days after their emergence, the reaction of resident ants exhibited a progressive increase in aggression, consistent with the age of the callows. Finally, even when callows were adopted in the foreign colony, they were still tolerated by their original colony when reintroduced. Taken together, these results show the complexity and precision of ants' recognition system.

Despite the complexity of this ability to recognize strangers and react aggressively to them, rescue behavior would appear even more complex: In rescue behavior experiments, ants' precisely directed behavior—in particular their ability to identify what, exactly, holds the victim in place and to adjust their behavior to that object in particular—reveals surprising cognitive capacities. What kinds of mechanisms would enable ants—and, indeed, ants from very different taxa—to recognize the difference between a nylon thread and a live predatory antlion, enabling them to sting the antlion but not the thread? Interestingly, during the field research with different species of Mediterranean ants, when repeated bites at the thread did not release the victim, rescuers sometimes flipped the exposed filter paper over and bit at the knot that held the thread in place (Hollis and Nowbahari, 2013; personal observations). Although the initial response to the SOS signal, which elicits frantic behavior in rescuers as they attempt to hone in on the direction of the victim, as well as limb pulling and digging behavior, could be released directly by a chemical call for help and thus result from a relatively simple mechanism, it's difficult to see how this same simple releasing mechanism could guide rescuers to the object that binds their nestmates and enables them to target and adjust their behavior to that object.

These studies also make clear that ants do not react as simple automatons. Their behavior is the result of a prepared program (genetic predisposition) as well as their social experience. One concept that might help us to understand some of these mechanisms is the *response threshold* (Page and Erber, 2002). In short, individual neurons respond to different stimuli and the resulting reactions are based on stimulus threshold. When a stimulus is below the critical threshold, no reaction is elicited but, if above, it provokes a reply. At the neuronal level, when a stimulus sufficiently depolarizes the membrane, an action potential is generated and the action potential propagates at full intensity. This theory is an attempt to explain the division of labor in insect social colony, through differences in the task-related response threshold of individuals. Division of labor within a honeybee colony is supposedly based on a response threshold for specific stimuli. Stimuli below a particular threshold result in no response for specific task, while stimuli above a threshold can elicit a reaction to it (Robinson, 1992; Page and Erber 2002; Beshers and Fewell, 2001). As Scheiner and Erber (2009) have described, all these myriad behavioral interactions are controlled by the relatively small nervous system of each individual. At first sight, it seems very difficult to analyze the neuronal mechanism underlying the complex organization of social behavior and the diversities of individual behavior, but the mechanism underlying social behavior can be directly tested by behavioral and neuronal sciences (Stark et al., 1998; Scheiner, 2004; Ozaki et al., 2005; Giurfa, 2007; Yamagata et al., 2007).

In sum, social life has forced ants to anticipate the behavior of conspecifics and cooperate or manipulate them. This anticipation requires complex communication mechanisms, favored by natural selection and thus closely related to the environment in which ants evolve, the particular problems they encounter, and the solutions that they bring to them. The study of these communication systems will help us to better understand not only ants' evolution, but also the means by which many species, from ants to primates, are able to engage in prosocial behavior.

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Note

1 Our use of the terms "altruism" and "prosocial" are likely very different from their use in anthropological and social psychological writing. Here, we use it in the biological sense as defined by Hamilton (1964), Trivers (1971) and Zahavi (1995).

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