



Sociobiology

An international journal on social insects

RESEARCH ARTICLE - ANTS

Do Odontomachus brunneus Nestmates Request Help and Are Taken Care of When Caught?

LUIZ C SANTOS-JUNIOR^{1,2}, EMERSON P SILVA³, WILLIAM F ANTONIALI-JUNIOR²

1 - Programa de Pós-graduação em Entomologia e Conservação da Biodiversidade, Universidade Federal da Grande Dourados, Dourados-MS, Brazil

2 - Laboratório de Ecologia Comportamental, Universidade Estadual de Mato Grosso do Sul, Dourados-MS, Brazil

3 - Museu da Biodiversidade, Universidade Federal da Grande Dourados, Dourados-MS, Brazil

Article History

Edited by

Kleber Del-Claro, UFU, Brazil

Received 24 November 2020

Initial acceptance 24 March 2021

Final acceptance 17 May 2021

Publication date 13 August 2021

Keywords

Poneromorph; Rescuers, Intraspecific Recognition; Rescue.

Corresponding author

Luiz C. Santos Junior

Programa de Pós-graduação em Entomologia e Conservação da Biodiversidade, Universidade Federal da Grande Dourados

Rodovia Dourados/Itahum, Km 12

Unidade II, Caixa Postal: 364

CEP: 79804-970 - Dourados-MS, Brasil.

E-Mail: lc.santosjunior@yahoo.com.br

Abstract

In social insects, situations can arise that threaten an individual or an entire colony. When the call for help goes out, different behavioral responses are elicited by signals emitted from nestmates. In ants, the response can be one of redemptive behavior by the worker receiving it. However, little is known about the evolution of this behavior and in which group of ants it manifests. Therefore, this study investigates whether workers of *Odontomachus brunneus* Patton can act as rescuers, able to detect and respond to calls for help from nestmates. Laboratory experiments were carried out in which the legs of ants were trapped by tape, simulating capture by a predator. Nearby nestmates were able to receive and respond to a request for help. Two experiments were performed: 1. Calls for help were made at different distances, in order to test the response latency. 2. Evaluation of whether rescuers would respond differently to calls for help from nestmates, non-nestmates of the same species, and ants of another species. Finally, evaluation was made of the behaviors of the rescuers when they responded to requests for help from nestmates and ants of another species. It could be concluded from the results that *O. brunneus* workers respond to signals emitted by workers who may have been captured by a potential predator, prompting the performance of behaviors related to rescue attempts. The signals involved appear to have an optimal range and are species-specific. When exposed to a capture situation, this species transmits audible signals by stridulation, so it is possible that this type of signal may be involved, in addition to chemical signaling.

Introduction

One of the benefits of living in social groups is the availability of defense, and one of the most effective ways of group defense is attacking the presumed predator (Siebenaler & Caldwell, 1956; Vogel & Fuentes-Jiménez, 2006). For example, wasp and bee colonies can group attack a potential predator, usually mobilized by volatile chemicals, such as the alarm pheromone (Morse & Laigo, 1969; Breed et al., 1990, 2004).

In some groups of ants, the morphologically modified caste of larger workers has, among other functions, the role of group defense when the colony is put under possible threat from an invader (Wilson, 1976; Hölldobler & Wilson, 1990; Powell & Clark, 2004; Pepper & Herron, 2008; Powell, 2008; Hou et al., 2010; Strassmann & Queller, 2010). Ants defend their colonies using various structures, when threatened by an individual from outside of the colony. In this way, bites and stings are commonly used in coordinated attacks



(Hölldobler & Wilson, 1990), as a strategy for group defense of the colony.

Some ant species have developed a unique means of defending themselves (Beponis et al., 2014). If an ant is caught, nestmates may exhibit rescue behavior to save it (Czechowski et al., 2002; Nowbahari et al., 2009; Nowbahari & Hollis, 2010; Miler, 2016). This behavior can be exhibited by one or more workers, known as first responders, and is directed towards another individual (the victim), in order to rescue it from a predator situation (Nowbahari & Hollis, 2010; Miler, 2016). Such behavior can involve relatively simple digging around the victim, with pulling of its limbs, to more precise behaviors such as directly attacking and stinging the trapping animal or object (Taylor & Visvader, 2013; Miler, 2016).

Independent of the species that can perform this type of behavior, there must be some exchange of signals between the ant that is requesting help and the rescuers. Ants and other social hymenopterans can produce and release volatile substances in the form of pheromones (Wheeler & Blum, 1973; Jafé & Marcuse, 1983; Lahav et al., 1999; Morgan et al., 1999; Lenoir et al., 2001; Hernández et al., 2002; Howard & Blomquist, 2005; Blomquist & Bagnères, 2010; Sainz-Borgo et al., 2011). They can also emit acoustic signals (Markl, 1973; Golden & Hill, 2016), such as those produced by the stridulatory organ, located between the petiole and the gaster in ants (Markl, 1973; Taylor, 1978; Stuart & Bell, 1980; Hölldobler & Wilson, 1990; Golden & Hill, 2016). This organ emits a “beep” that has different roles in the functioning of the colony (Markl & Hölldobler, 1978; Chiu et al., 2011).

In the *Odontomachus* genus, workers, in particular, produce sounds in the form of stridulation, when they feel threatened (Markl, 1973; Golden & Hill, 2016). Therefore, it is likely that ants of the species *Odontomachus brunneus* Patton, 1894 may emit this type of signaling as a way of recruiting their nestmates, when they are exposed to a dangerous situation. The signaling may involve chemicals, sound signals, or a combination of both methods.

Most of the studies on this topic have been performed for ants inhabiting sandy areas, with exposure to lion ant larvae (Neuroptera: Myrmeleontidae). This relationship seems to have contributed to the evolution of rescue behavioral patterns that prevail in ants, especially in species of the genera *Cataglyphis*, *Formica*, and *Lasius*, all belonging to the subfamily Formicinae (Gotelli, 1996; Czechowski et al., 2002; Hollis & Nowbahari, 2013a; Miler, 2016; Hollis, 2017). However, studies show that ants from other subfamilies, such as Myrmicinae and Ponerinae, are also capable of exhibiting some kind of rescue behavior (Hollis & Nowbahari, 2013a; Frank et al., 2017, 2018). Hence, the occurrence of rescue behavior in relatively unrelated ant species suggests that this behavior is not phylogenetically restricted and that many factors may contribute to its occurrence.

Unfortunately, little is known about rescue behavior in poneromorph ants. Therefore, the aim of this study was to

evaluate whether workers of *O. brunneus*, when exposed to a capture situation, emit some kind of signal that provokes help in the form of attempted rescue by nestmates.

Materials and Methods

Six colonies of *O. brunneus* were collected in the urban area of Dourados, in Mato Grosso do Sul State, Brazil (22°13'16" S; 54°48'20" W), between September 2016 and September 2017.

All the ants were collected from hollow trunks of *Caesalpinia pluviosa* (Fabaceae), using tweezers, and were placed in plastic pots. In the laboratory, the ants were housed in artificial nests constructed using plastic trays (10 x 20 cm). Inside there were plaster molds that simulated the nest chambers, which were connected to a foraging arena, where food was offered to the colonies.

The colonies were kept at a controlled temperature of around 25.0 ± 1 °C, relative humidity of $65 \pm 5\%$, and 12-hour photoperiod, for a seven-day habituation period, and were fed *ad libitum* with water and honey on moistened cotton inside an Eppendorf tube. As a protein source, last instar *Tenebrio molitor* Linnaeus, 1758 larvae were offered every five days. The behavioral tests were performed after the habituation period.

Latency time and call for help to nestmate rescuer ants

Tests were conducted in order to understand if *O. brunneus* first responders could respond to their nestmates call for help, by simulating capture at different distances from the first responders.

A system of plastic chambers and connectors (15 x 10 x 8 cm) was constructed, allowing for the insertion of rescuers and a trapping chamber (10 x 8 cm) where an ant was attached to simulate its capture. These two sites were connected by a tube 2 cm in diameter and with different lengths (30, 60, and 90 cm), in order to assess whether the call for assistance might vary as a function of distance (Fig 1).

Ten foraging workers were inserted in the arena as potential rescuers. In the trapping chamber, a forager from the same colony was secured by tape, following the modified methodology used in rescue behavior studies by artificial imprisonment in ants (Nowbahari et al., 2009, 2012, 2016; Hollis & Nowbahari, 2013a; Duhoo et al., 2017). Prior to each test, the arena, the trapping chamber, and the connector tube were sterilized with an alcohol-soaked filter paper. The tests were conducted under laboratory conditions, at a constant temperature of 25.0 ± 1 °C and humidity of $65 \pm 5\%$.

For each of the three different connector distances, 30 different ant groups were tested, with each group including 10 rescuers and 1 trapped ant. In each test, the observation time was 15 min, from the moment the ant was immobilized in the trapping chamber and all the rescuers were released into the arena. At the end of each test, the number of rescuers entering the trapping chamber was counted, so it was possible to assess

whether distance was a factor affecting the number of ants able to respond to the call for help.

Rescuer latency in responding to the call for aid was calculated as described by Nowbahari et al. (2016). This was defined as the period between the time of entry of the

first rescuer into the connector tube and the time of the first attempt at rescuing the trapped ant performed by that rescuer.

As a control, the same parameters were measured under the same conditions and with the same group of ants used in each test, but without the ant in the trapping chamber.

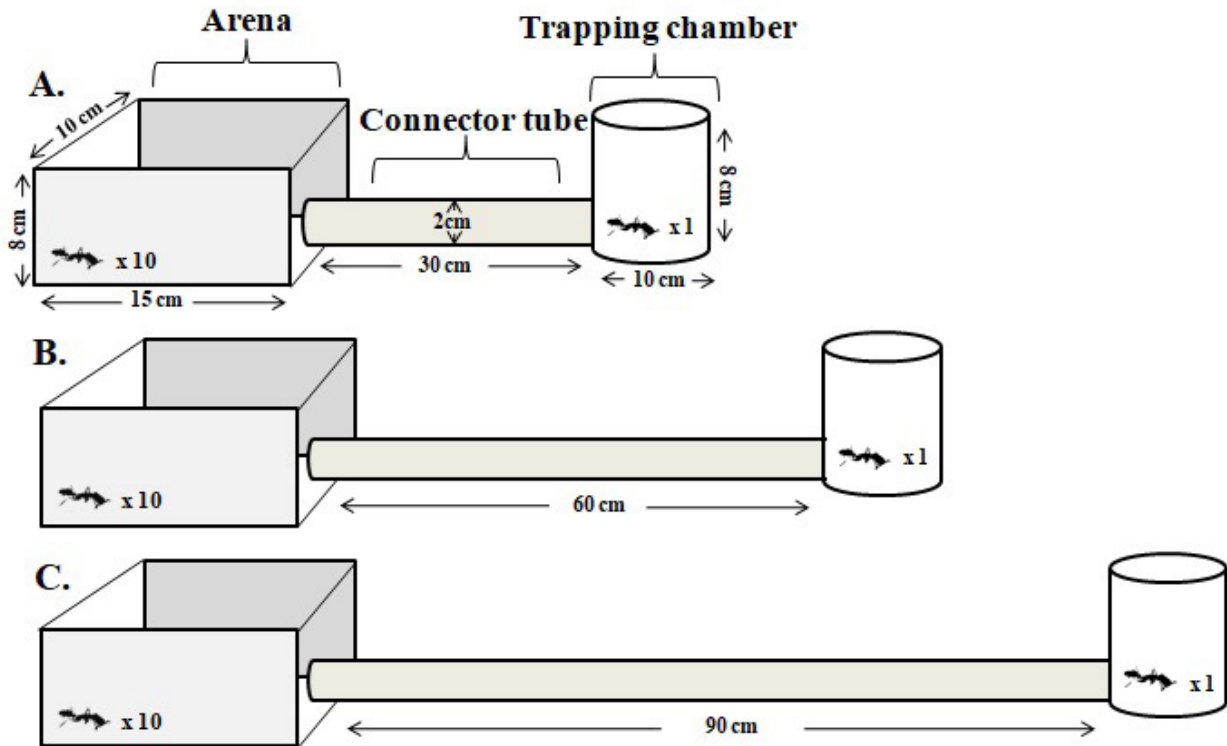


Fig 1. Scheme used for the latency tests of rescue behavior between *O. brunneus* nestmates. A: Arena connected to the trapping chamber through a 30 cm connector tube; B: Arena connected to the trapping chamber through a 60 cm connector tube; C: Arena connected to the trapping chamber through a 90 cm connector tube.

Test to evaluate the specificity of the response to help requests

Three different help request situations were simulated, in order to evaluate whether workers from a particular colony might respond to a request for help from non-nestmate ants (Nowbahari & Hollis, 2010; Miler, 2016; Uy et al., 2018).

The chamber system and connectors used in this test were adapted from Yusuf et al. (2014). The system included an arena where 10 rescuers were inserted, connected to a tube 25 cm long and 2 cm in diameter, the end of which had a connector allowing bifurcation into two other tubes, each 5 cm long and with the same diameter. Each led to a plastic trapping chamber (10 x 8 cm), where at least one of them had a nestmate attached by tape. Then, either a rescue ant from the same colony was inserted, or an ant from another colony and/or species was inserted (Fig 2).

In each test, the observation time was 15 min, from the moment the ants were trapped in the imprisonment chambers and all the rescuers were released into the arena.

Three types of experiments were conducted. In the first, rescuers were tested for their ability to receive the call

for help and respond to it, using a Y-maze system. For this, an *O. brunneus* nestmate worker was fixed in only one of the entrapment chambers (Fig 2-A), while the other chamber contained a loose nestmate. In the second experiment, rescuers were tested for their ability to distinguish between the requests for help made by a nestmate and a non-nestmate. For this test, a nestmate was trapped in one imprisonment chamber, while the other chamber contained a trapped non-nestmate (Fig 2-B). In the third experiment, a nestmate was immobilized in one entrapment chamber, while the other contained a worker of another species, in this case *Odontomachus chelifer*, Latreille, 1802 (Fig 2-C). Each of the three experimental designs was performed using thirty tests with different groups of rescuers and trapped workers.

All the behaviors exhibited by the rescuers upon entering the trapping chamber were observed and described according to the methodology of Nowbahari et al. (2016). To obtain the average frequency of each behavioral act performed by the rescuers, the behaviors at the end of all the tests were summed and divided by the sum of execution of all the behavioral acts.

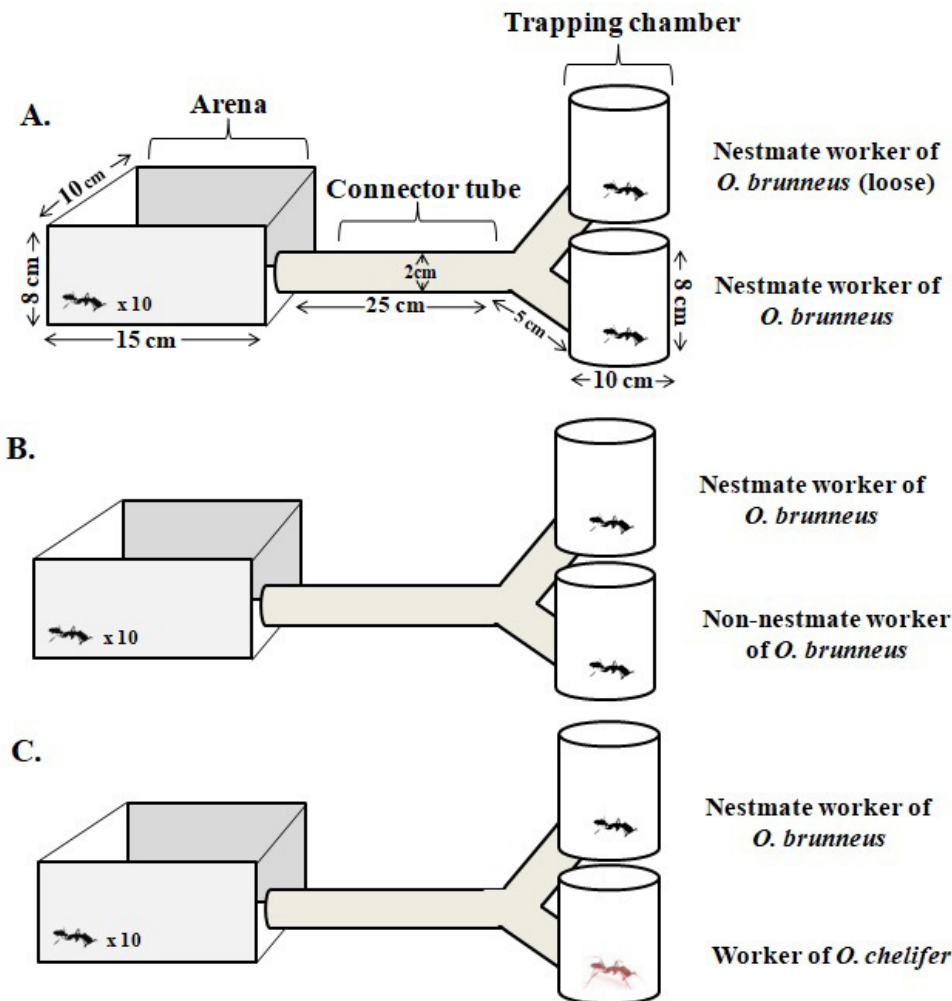


Fig 2. Scheme used for the Y-maze decision tube tests with the rescue workers in the arena and the workers in the trapping chambers. A: Test with nestmate workers loose and trapped in the trapping chambers; B: Test with a trapped nestmate worker in one chamber and a trapped non-nestmate worker in the other chamber; C: Test with a trapped nestmate in one of the chambers and a trapped *O. chelifera* worker in the other chamber.

Statistical analysis

Differences among the treatments and the controls were evaluated using the Student's *t*-test applied to the average values for the number of rescuers remaining in the trapping chamber in the tests performed with the connectors of three different lengths (distances).

The same test was used to evaluate differences between the average latency times of the rescuers in answering the requests for help by the trapped workers in the tests performed with the different connectors, as well as when there was no trapped worker (controls).

The Kruskal-Wallis test was applied to determine any significant differences among the average latency times in responding to the request for help from a trapped worker, for the three different distances.

A *t*-test was applied to evaluate any significant differences among the mean values of the number of first responders that remained in the trapping chamber during the Y-maze decision tests.

Results

In all the tests, independent of distance, rescuers went to their nestmate and performed rescue behaviors, using bites and stings against the tape that held it. However, the number of rescuers reaching the trapping chamber was significantly higher when the distance was 30 cm. The average numbers of ants in the trapping chamber with the trapped ant and in the control situation are shown in Table 1.

The latency times showed that the rescuers took less time to respond to the call for help within 30 cm. At this distance, there was a significant difference between the times recorded with an ant trapped in the chamber and with no ant (Table 2).

In the tests to assess specificity in responding to requests for help, the rescue workers opted for a trapping chamber containing a trapped worker from the same colony, as opposed to a nestmate loose in a chamber and/or an ant of another species in the chamber. No significant differences were found between the numbers of times rescuers opted for a chamber

Table 1. Average numbers of rescue ants attending nestmates trapped at different distances.

	DISTANCE					
	30 cm		60 cm		90 cm	
	With ant	Without ant	With ant	Without ant	With ant	Without ant
Average number of rescuers	8.73 ± 1.05	1.53 ± 1.66	3.53 ± 1.31	3.33 ± 1.49	3.03 ± 1.27	2.06 ± 1.54
p-value	<0.001		0.54		0.16	
t-test	21.81		0.61		1.43	

Table 2. Average latency times of rescue ants present in the capture chamber positioned at different distances.

	DISTANCE					
	30 cm		60 cm		90 cm	
	With ant	Without ant	With ant	Without ant	With ant	Without ant
Latency (minutes)	0:29 ± 0.01	2:43 ± 0.01	3:00 ± 0.02	3:03 ± 0.02	9:27 ± 0.21	8:52 ± 0.20
p-value	<0.0001		0.732		0.955	
t-test	-2.5		0.34		0.05	

with a nestmate, compared to a chamber with a non-nestmate (Table 3). The behaviors exhibited by the rescuers when they arrived at the trapping chamber are described in Table 4.

The behaviors suggested that some kind of rescue was only performed to assist either a nestmate or a non-nestmate of the same species (Table 4).

Table 3. Average numbers of rescue ants present in the trapping chambers when an ant was trapped on one side of the connector tube.

	DECISION TEST					
	Nestmate (trapped)	Nestmate (loose)	Nestmate	Non-nestmate	Nestmate	<i>O. chelifera</i>
Average number of rescuers	8.1 ± 1.24	1.00 ± 1.31	5.33 ± 3.45	4.13 ± 3.61	7.60 ± 1.67	1.06 ± 1.17
p-value	<0.001		0.35		<0.001	
t-test	0.80		0.93		1.31	

Discussion

The range of signals involved was even more evident from analysis of the significant differences between the distances in terms of latency time. Alarm pheromones are volatile chemical compounds used for communication by various social insects (Crewe et al., 1972; Traniello, 1982; Blomquist & Bagnères, 2010). These include various species of less derived ants (Robertson, 1971; Hölldobler & Taylor, 1983; Hölldobler & Wilson, 1990), such as *O. bauri* (Sainz-Borgo et al., 2011). Hölldobler and Wilson (1990) reported that these alarm pheromones are transmitted over short distances and are coded by workers able to respond in various ways, such as by attacking. The diffusion model of Bossert and Wilson (1963) predicts that the alarm pheromone emitted by ants can reach a radius of approximately 20cm, in the absence of a draft. Therefore, in this study, if the ants responded only to chemical signals, the range of these compounds would be greater, since some response occurred

even at a distance of 90 cm. However, it should be noted that the testing employed a chamber-and-tube system, which may have reduced dispersion and assisted the targeting of the volatile compounds.

Another consideration is that when immobilized, the workers of *O. brunneus* make an audible sound produced by stridulation. Although this would need to be tested, it should be highlighted here that the workers could emit this complementary signal, in order to enlist help. This acoustic signal is produced by friction between the petiole and the gaster (Markl, 1965; Taylor, 1978; Hölldobler & Wilson, 1990; Grasso et al., 2000), as observed previously in ants of this genus (Markl, 1973; Golden & Hill, 2016). Among other functions, these signals emitted by ants may be a call for help, as indicated in several ant rescue behavior studies (Czechowski et al., 2002; Nowbahari et al., 2009; Nowbahari & Hollis, 2010; Miler, 2016; Frank et al., 2017, 2018). Therefore, it is possible that nestmates may have emitted a chemical and/or audible signal that was coded by rescuers,

enabling rescue behavior to be directed towards their nestmates. The evidence suggested that the first responders could have responded to the call for help at distances greater than reported in the literature (Bossert & Wilson, 1963).

In contrast, the number of first responders responding to the request for help by the ant in the trapping chamber decreased significantly as the distance increased. Recent work has evidenced rescue behavior among nestmates in poneromorph ants (Frank et al., 2017, 2018), but no available data could be found describing the maximum distance of such signaling. Rescue behavior in ants was discussed by Hollis and Nowbahari (2013b), who demonstrated that a greater number of workers involved in the rescue attempt could improve the chances of success. Group defensive behavior in social insects, especially ants, is a well-known phenomenon (Hölldobler & Wilson, 1990) and includes rescue behavior (Czechowski et al., 2002; Hollis & Nowbahari, 2013a; Hollis et al., 2015; Frank et al., 2017). The present results suggested that distance could be a major factor determining the number of ants recruited for rescue, indicating that distance may be a key factor influencing rescue success. In this case, it appeared that the request for help would receive a better response if the captured ant was not more than 30 cm distant, corresponding to relatively close proximity to the entrance of the nest, if the ant was captured outside it.

The emission of signals by the captured ant is a major determinant of rescue success. Miler (2016) evaluated rescue behavior among nestmates of *Formica cinerea*, comparing capture by the lion ant (*Myrmeleon bore*) with artificial capture, from which it was concluded that the latency time was shorter for artificially captured ants. When ants are captured by a lion ant, they are anesthetized by the action of the chemical compound injected by the Myrmeleontidae. For this reason, the ants are slow to emit a help signal, resulting in a longer latency time for rescue. It was also concluded that the longer latency time in the aid request resulted in a lower expectation of rescue, compared to ants who promptly issued the aid request (Miler, 2016).

The results also suggested that the signals involved are similar between colonies of the same species. The rescue workers responded to requests for help from nestmates and non-nestmates, without any significant difference. Previous

studies with ants have also reported this rescue behavior for non-nestmates (Taylor et al., 2013; Uy et al., 2018). However, in studies of such behavior in the ant *Oecophylla smaragdina* Fabricius, 1775, Uy et al. (2018) concluded that colonies with greater similarity in odor models could present a recognition error, with non-nestmates likely to be confused with nestmates, consequently being rescued. In this way, colonies that are closer are more likely to be genetically related, resulting in greater tolerance among the nearest colonies, which increases the possibility of rescuing non-nestmates (Errard et al., 2006; Newey et al., 2010; Uy et al., 2018). This provides an explanation for the fact that the *O. brunneus* first responders responded to requests for help from non-nestmates, as well as from nestmates, since the colonies were collected at relatively close distances.

On the other hand, the rescue workers responded to the request for help from *O. chelifera* ants with aggressive behaviors, stinging and biting the immobilized ant (Table 4). This was different from how they acted when helping the ants of the same species, when the rescuers delivered bites and stings to the duct tape, suggesting an attempt to free their nestmate. These results corroborated those of Hollis and Nowbahari (2013a), who investigated the requests for help using five different species of ants, finding that all of them rescued their co-specifics, but not ants of other species, in the latter case also being aggressive towards the immobilized ant. The evidence suggests that the signals involved in this type of behavior are specific, at least at the species level. However, further analysis is needed to assess the level of specificity, since rescue behavior is onerous for the ants that perform it, and rescuing an ant from another colony without a degree of kinship would not make sense from an evolutionary point of view.

It could be concluded from the results obtained in this work that *O. brunneus* workers respond to signals emitted by a worker who may have been captured by a potential predator, leading to an attempt at rescue. The signals involved seem to have an optimal range, in addition to being species-specific. This species emits sound signals by stridulation, when exposed to a capture situation, suggesting that this type of signal may be involved, in addition to chemical signals. However, further experiments will be necessary to test this possibility.

Table 4. Frequencies of behaviors exhibited during interactions between rescue workers and the trapped ant in the decision-making experiments.

Behaviors of rescue workers	FREQUENCY DURING THE MEETING (%)					
	Nestmate (loose)	Nestmate (trapped)	Nestmate	Non-nestmate	<i>O. brunneus</i>	<i>O. chelifera</i>
Recognition of the trapped individual	0.00	40.32	36.25	33.87	49.56	56.25
Pull the trapped individual with the jaws	0.00	0.00	0.00	0.00	0.00	0.00
Bite or pull the tape with the jaws	0.00	13.16	19.37	23.38	17.98	6.25
Sting or bite the trapped individual	0.00	0.00	0.00	0.00	0.00	34.37
Sting the tape	0.00	46.50	44.37	42.74	32.45	3.12

Acknowledgments

The authors thank Fundação de Apoio ao Desenvolvimento do Ensino Ciência e Tecnologia do Estado de Mato Grosso do Sul (FUNDECT) for a doctoral scholarship awarded to the third author (FUNDECT n° 03/2014), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for doctoral scholarships awarded to the first and second authors, and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for a productivity scholarship (WFAJ, grant number 307998/2014-2).

Author contributions

Conceived and designed the experiments: Santos-Junior, L.C. & Antonialli-Junior, W.F.; Performed the experiments: Santos-Junior, L.C. & Silva, E.P.; Analyzed the data: Santos-Junior, L.C., Silva, E.P., & Antonialli-Junior, W.F.; Wrote the paper: Santos-Junior, L.C. & Antonialli-Junior, W.F.

References

- Breed, M.D., Guzmán-Novoa, E. & Hunt, G.J. (2004). Defensive behavior of honey bees: Organisation, genetics, and comparison with other bees. *Annual Review of Entomology*, 49: 271-298. doi: 10.1146/annurev.ento.49.061802.123155
- Breed, M.D., Robinson, G.E. & Page R.E.-Jr. (1990). Division of labor during honeybee colony defense. *Behavioral Ecology and Sociobiology*, 27: 395-401
- Beponis, L.M., O'Dea, R.E., Ohl, V.A., Ryan, M.P., Backwell, P.R.Y., Binning, S.A. & Haff, T.M. (2014). Cleaning up after a meal: The consequences of prey disposal for pit-building antlion larvae. *Ethology*, 120: 873-880. doi: 10.1111/eth.12257
- Bossert, W.H. & Wilson, E.O. (1963). The analysis of olfactory communication among animals. *Journal of Theoretical Biology*, 5: 443-469 doi: 10.1016/0022-5193(63)90089-4
- Blomquist, G.J. & Bagnères, A.G. (2010). *Insect Hydrocarbons Biology, Biochemistry, And Chemical Ecology*. Cambridge University Press, 528 p.
- Chiu, Y.K., Mankin, R.W. & Lin, C.C. (2011). Context-dependent stridulatory responses of *Leptogenys kitteli* (Hymenoptera: Formicidae) to social, prey, and disturbance stimuli. *Annals of the Entomological Society of America*, 104: 1012-1020. doi: 10.1603/an11027
- Czechowski, W., Godzińska, E.J. & Kozłowski M.W. (2002). Rescue behavior shown by workers of *Formica sanguinea* Latr., *F. fusca* L. and *F. cinerea* (Hymenoptera: Formicidae) in response to their nestmates caught by an ant lion larva. *Annales Zoologici*, 52: 423-431
- Crewe, R.M., Blum, M.S. & Collingwood, C.A. (1972). Comparative analysis of alarm pheromones in the ant genus *Crematogaster*. *Comparative Biochemistry and Physiology*, 43: 703-716. doi: 10.1016/0305-0491(72)90155-1
- 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. doi: 10.1016/j.beproc.2017.02.006
- Errard, C., Hefetz, A. & Jaisson, P. (2006). Social discrimination tuning in ants: template formation and chemical similarity. *Behavioral Ecology and Sociobiology*, 59: 353-363. doi: 10.1007/s00265-005-0058-z
- 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: e1602187. doi: 10.1126/sciadv.1602187
- 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: 1-8. doi: 10.1098/rspb.2017.2457
- Grasso, D.A.T., Wenseleers, T., Mori, A., Moli, F. & Billen, J. (2000). Thelytokous worker reproduction and lack of *Wolbachia* infection in the harvesting ant *Messor capitatus*. *Ethology Ecology and Evolution*, 12: 309-314. doi: 10.1080/08927014.2000.9522803
- Golden, T.M.J. & Hill, P.S. (2016). The evolution of stridulatory communication in ants, revisited. *Insectes Sociaux*, 63:309-319 doi: 10.1007/s00040-016-0470-6
- Gotelli, N.J. (1996). Ant community structure: Effects of predatory ant lions. *Ecology*, 77: 630-638. doi: 10.2307/2265636
- Hernández, J.V., Lopez, H. & Jaffé, K. (2002). Nestmate recognition signals of the leaf cutting ant *Atta laevigata*. *Journal of Insect Physiology*, 48: 287-295. doi: 10.1016/S0022-2973 1910(01)00173-1
- Hölldobler, B. & Taylor, R.W. (1983) A behavioral study of the primitive ant, *Nothomyrmecia macrops* Clark. *Insectes Sociaux*, 30: 384-401. doi: 10.1007/BF02223970
- Hölldobler, B. & Wilson, E.O. (1990). *The Ants*. Cambridge: Harvard University Press, 732 p
- Hollis, K.L. (2017). Ants and antlions: The impact of ecology, coevolution and learning on an insect predatory prey relationship. *Behavioural Processes*, 139: 4-11. doi: 10.1016/j.beproc.2016.12.002
- Hollis, K.L. & Nowbahari, E. (2013-a). A comparative analysis of precision rescue behavior in sand-dwelling ants. *Animal Behaviour*, 85: 537-544. doi: 10.1016/j.anbehav.2012.12.005
- Hollis, K.L. & Nowbahari, E. (2013-b). Toward a behavioral ecology of rescue behavior. *Evolutionary Psychology*, 11: 647-664. doi: 10.1177/147470491301100311

- Howard, R.W. & Blomquist, G.J. (2005). Ecological, behavioral, and biochemical aspects of insect hydrocarbons. *Annual Review of Entomology*, 50: 371-393. doi: 10.1146/annurev.ento.50.071803.130359
- 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 Motivation* 50: 68-82. doi: 10.1016/j.lmot.2014.11.003
- Hou, C., Kaspari, M., Zanden, H.B.V. & Gillooly, J.F. (2010). Energetic basis of colonial living in social insects. *Proceedings of the National Academy of Sciences*, 107: 3634-3638. doi: 10.1073/pnas.0908071107
- Jaffé, K. & Marcuse, M. (1983). Nestmate recognition and territorial behaviour in the ant *Odontomachus bauri* Emery (Formicidae: Ponerinae). *Insectes Sociaux*, 30: 466-481
- Lahav, S., Soroker, V., Hefetz, A. & Vander-Meer, R.K. (1999). Direct behavioral evidence for hydrocarbons as ant recognition discriminators. *Naturwissenschaften*, 86: 246-249. doi: 10.1007/s001140050609
- Lenoir, A., Hefetz, A., Simon, T. & Soroker, V. (2001). Comparative dynamics of gestalt odour formation in two ant species *Camponotus fellah* and *Aphaenogaster senilis* (Hymenoptera: Formicidae). *Physiological Entomology*, 26: 275-283. doi: 10.1046/j.0307-6962.2001.00244.x
- Markl H., Hölldobler B. (1978). Recruitment and food-retrieving behavior in *Novomessor* (Formicidae, Hymenoptera): II vibration signals. *Behavioral Ecology and Sociobiology*, 4: 183-216
- Markl, H. (1965). Stridulation in leaf-cutting ants. *Science*, 149: 1392-1393 doi: 10.1126/science.149.3690.1392
- Markl, H. (1973). The evolution of stridulatory communication in ants. In: *International Union for the Study of Social Insects (7th), Proceedings*. London, 258-265 p.
- Miler, K. (2016). Moribund ants do not call for help. *PLoS One* 11: e0151925 doi: 10.1371/journal.pone.0151925
- Morse, R.A. & Laigo, F.M. (1969). *Apis dorsata* in the Philippines. *Philippine Association of Entomologists*, 1: 1-96
- Morgan, E.D., Nascimento, R.R., Keegans, S.J. & Billen, J. (1999). Comparative study of mandibular gland secretions of workers of ponerine ants. *Journal of Chemical Ecology*, 25: 1395-1409. doi: 10.1023/A:1020987028163
- Nowbahari, E., Amirault, C. & Hollis, K.L. (2016). Rescue of newborn ants by older *Cataglyphis cursor* adult workers. *Animal Cognition*, 19: 543-553. doi: 10.1007/s10071-016-0955-8
- 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: e48516. doi: 10.1371/journal.pone.0048516
- Nowbahari, E., Scohier, A., Durand, J. & Hollis, K.L. (2009). Ants, *Cataglyphis cursor*, use precisely directed rescue behavior to free entrapped relatives. *PLOS One*, 4: e6573. doi: 10.1371/journal.pone.0006573 PMID: 19672292
- Nowbahari, E. & Hollis, K.L. (2010). Rescue behavior. Distinguishing between rescue, cooperation and other forms of altruistic behavior. *Communicative and Integrative Biology*, 3: 77-79. doi: 10.4161/cib.3.2.10018 PMID: 20585494
- Newey, P.S., Robson, S.K.A. & Crozier, R.H. (2010). Weaver ants *Oecophylla smaragdina* encounter nasty neighbors rather than dear enemies. *Ecology*, 91: 2366-2372. doi: 10.1890/09-0561.1
- Powell, S. & Clark, E. (2004). Combat between large derived societies: A subterranean army ant established as a predator of mature leaf-cutting ant colonies. *Insectes Sociaux*, 51: 342-351. doi: 10.1007/s00040-004-0752-2
- Powell S. (2008). Ecological specialization and the evolution of a specialized caste in *Cephalotes* ants. *Functional Ecology*, 22: 902-911. doi: 10.1111/j.1365-3046.2008.01436.x
- Pepper, J.W. & Herron, M.D. (2008). Does biology need an organism concept? *Biological Reviews*, 83: 621-627. doi: 10.1111/j.1469-185X.2008.00057.x
- Robertson, P.L. (1971). Pheromones involved in aggressive behaviour in the ant *Myrmeciagulosia*, ft. *Journal of Insect Physiology*, 17: 691-715. doi: 10.1016/0022-1910(71)90117-X
- Siebenaler, J.B. & Caldwell, D.K. (1956). Cooperation among adult dolphins. *Journal of Mammalogy*, 37: 126-128. doi: 10.2307/1375558
- Stuart, R.J. & Bell, P.D. (1980). Stridulation by workers of the ant *Leptothorax muscorum* (Nylander) (Hymenoptera: Formicidae). *Psyche*, 87: 199-210. doi: 10.1155/1980/46583
- Strassmann, J.E. & Queller, D.C. (2010). The social organism: congresses, parties, and committees. *Evolution*, 64, 605-616 doi: 10.1111/j.1558-5646.2009.00929.x
- Sainz-Borgo, C., Cabrera, A.E. & Hernández, J.V. (2011). Nestmate recognition in the ant *Odontomachus bauri* (Hymenoptera: Formicidae). *Sociobiology*, 58: 1-18 doi: 10.1007/BF02223978
- Taylor, K., Visvader, A., Nowbahari, E. & Hollis, K.L. (2013). Precision rescue behavior in North American ants. *Evolutionary Psychology*, 11: 665-677 doi: 10.1177/147470491301100312
- Taylor, F. (1978). Foraging behavior of ants: theoretical considerations. *Journal of Theoretical Biology*, 71: 541-565. doi: 10.1016/0022-5193(78)90324-7
- Traniello, J.F.A. (1982). Population structure and social organization in the primitive ant *Amblyopone pallipes* (Hymenoptera: Formicidae). *Psyche*, 89: 65-80. doi: 10.1155/1982/79349

Uy, F.M.K., Adcock, J.D., Jeffries, S.F. & Pepere, E. (2018). Intercolony distance predicts the decision to rescue or attack conspecifics in weaver ants. *Insectes Sociaux*, 66: 185-192. doi: 10.1007%2Fs00040-018-0674-z

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: 1012-1016. doi: 10.1002/ajp.20286

Wheeler, J.W. & Blum, M.S. (1973). Alkylpyrazine alarm pheromones in ponerine ants. *Science*, 182: 501-503 doi: 10.1126/science.182.4111.501

Wilson, E.O. (1976). A social ethogram of the neotropical arboreal ant, *Zacryptocerus varians* (Fr. Smith). *Animal Behaviour*, 24: 354-363. doi: 10.1016/S0003-3472(76)80043-7

Yusuf, A.A., Crewe, R.M. & Pirk, C.W. (2014). Olfactory detection of prey by the termite-raiding ant *Pachycondyla analis*. *Journal of Insect Science*, 14: 53 doi: 10.1093/jis/14.1.53

