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ORIGINAL ARTICLE

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Polyethism and the importance of context in the alarm reaction of the grass-cutting ant, *Atta capiguara*

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Abstract Leaf-cutting ants exhibit an aggressive alarm response. Yet in most alarm reactions, not all of the ants encountering a disturbance will respond. This variability in behaviour was investigated using field colonies of *Atta capiguara*, a grass-cutting species. Crushed ant heads were applied near foraging trails to stimulate alarm reactions. We found that minor workers were disproportionately likely to respond. Only 34.7±2.8% of ants travelling along foraging trails were minor workers, but 82.1±6.1% of ants that responded were minors. Workers transporting grass did not respond at all. The alarm response was strongest at the position and time where minors were most abundant. Ants were more likely to respond when they were travelling along trails with low rather than high traffic. Minor workers followed a meandering route along the trail, compared with the direct route taken by foragers. We argue that an important function of minor workers on foraging trails is to patrol the trail area for threats, and that they then play the key role in the alarm reaction.

Keywords Leaf-cutting ants · *Atta capiguara* · Polyethism · Alarm behaviour · Context

Introduction

Division of labour in insect societies is based upon polyethism (Weir 1958; Wilson 1963), which is generally divided into two types: physical and temporal. In physical polyethism the castes are morphologically distinct, being normally of different sizes, while in temporal polyethism, individuals carry out different tasks at different times in their lives. The tendency for an individual to engage in a particular behaviour is affected by the context. Honey ants (*Myrmecocystus mimicus*), for example, have to be stimulated into an “excited” phase before they will respond to trail pheromone, and workers scouting for a new food source will not respond at all (Hölldobler 1981). Alarm behaviour is affected by both caste and context and can be divided into aggressive and panic responses. Panic alarm involves workers dispersing away from the source, while in an aggressive response, workers are attracted to and attack the source of the disturbance (Wilson and Regnier 1971). Most social insects show polyethism in their alarm response. Honey bee colonies have a subset of soldier bees that defend the colony (Breed et al. 1990), while in many ant species, it is the larger individuals that respond during an aggressive reaction (Hölldobler and Wilson 1990). Individuals commonly react more aggressively to disturbances that are close to the nest (Shorey 1973), and responsiveness can further vary depending on other stimuli received. For example, during the first 3 h after encountering a food source, workers of the ant *Crematogaster scutellaris* are in an excited state and have a raised threshold for the release of alarm behaviour (Leuthold and Schlunegger 1973).

Leaf-cutting ants (Hymenoptera: Formicidae: Attini: *Atta* and *Acromyrmex*) are dominant herbivores in the Neotropics and can be significant pests (Weber 1972; Cherrett 1986; Hölldobler and Wilson 1990). Certain species forage exclusively on monocotyledonous plants and are termed grass-cutting ants, but their biology is very similar to the species that harvest dicotyledonous plants. Leaf-cutting ants form colonies of up to 7 million workers (Jonkman 1980) with high levels of polymorphism and polyethism. The workers are not discontinuous in size but they can be divided into four alloethic groups; minors, medias, foragers and soldiers (Wilson

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1980a). The minors and medias are generally described as engaging in within-nest tasks. However, both may be found on the foraging trails in large numbers where their role is uncertain, because they are too small to transport vegetation (Stradling 1978; Wilson 1980b). The suggestion has been made that they defend their larger nestmates against parasitic phorid flies (Eibl-Eibesfeldt and Eibl-Eibesfeldt 1967; Feener and Moss 1990; Orr 1992). Transporting ants are particularly vulnerable, so the minor workers are thought to "hitchhike" on the pieces of vegetation being transported and drive away flies that attempt to parasitise the transporting ant.

When disturbed, leaf-cutting ants exhibit an aggressive alarm reaction and release an alarm pheromone from their mandibular glands (Blum et al. 1968; Moser et al. 1968; Riley et al. 1974). The occurrence of polyethism in the defence reaction has been implicitly recognised by terming the largest workers "soldiers" (Weber 1972) or "defenders" (Wilson 1980a). These soldiers have greatly enlarged mandibular muscles for biting, and their only role is colony defence (Weber 1972; Wilson 1980a). However, studies on laboratory colonies have found that ants of a wide size range respond during alarm reactions (Wilson 1980a; Vilela and Howse 1986), and soldiers are mainly found in the nest (Moser 1967). Very few studies have examined the alarm reaction of leaf-cutting ants on trails or under natural conditions.

This study examined the role of polyethism in the alarm response of field colonies of *Atta capiguara*. We established which castes were involved in alarm reactions on trails, and whether or not transporting workers also responded. We then examined whether the castes differed in their trail behaviour. In a third experiment, the effect of context on the alarm response was quantified, and we attempted to establish if any effects of context could be explained by variations in the behaviours and castes of the ants present.

Methods

These experiments were carried out during November 1997 and April–May 1998, on pastures located within 30 km of Capinópolis, in the west of the state of Minas Gerais, Brazil. All of the nests used were mature, with mound surface areas of at least 10 m^2.

Polyethism in the alarm reaction

Two alarm sources were used in this experiment: a whole ant with its head crushed, and a crushed head alone. The ants used as sources were foragers, with a head width of between 2.5 and 3 mm. They were taken from the experimental trail immediately prior to use, and the head was crushed using a clean metal rod. Blank rubber septa were used as the controls and each source was replicated ten times with different trails. The sources were placed 15 cm from the trail, at a point 1 m from the trail entrance hole, in the centre of a 10-cm-diameter circle (the "test area") that had been previously cleared of vegetation. These test areas were connected to the trail by 10-cm-wide "roads" that were also cleared of vegetation, so that the number of ants leaving the trail and travelling towards the source could be counted (see Fig. 1).

The strength of the alarm response was quantified by recording the numbers of ants travelling along the roads during 30 s, and the maximum number of ants within the test areas at any one time during a 30-s period. To confirm whether the response was due to a change in the behaviour of ants on the trails or a change in the overall ant traffic, the numbers of ants travelling along the trails during 30 s were counted. Trail counts were made either side of the junction with the road, and were averaged to give an estimate of the trail traffic. All counts were made immediately before the application of the source (time 0) and 2, 6 and 10 min afterwards. Ants were recorded as being either "minors" or "foragers" to establish if the castes differed in their responsiveness. Minors had a head width of less than 1.4 mm while foragers had a head width greater than this, and ants could be readily and reliably assigned to these classes by eye. Soldiers were virtually never observed on the trails and were not included in the analysis. We also recorded if the ants were transporting a load, in order to establish if transporting ants responded during the alarm reactions.

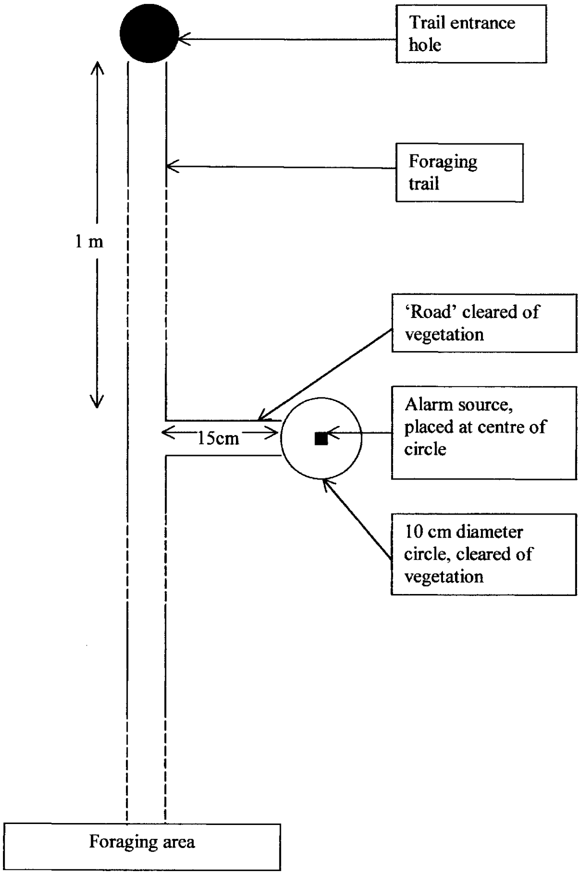

Fig. 1 Diagram of the set-up for the first experiment

The data were log transformed [or log (x+1) when there were zero counts] and analysed with one-way repeated-measures analyses of variance (ANOVAs). By examining the interaction between treatment and time, these tested the null hypothesis that the numbers of ants changed in the same way over the experimental period regardless of the treatment applied. The proportions of foragers and minors in the ant counts were compared with *G*-tests, with *G* adjusted with William's correction factor (Fowler and Cohen 1997).

Trail behaviour

During the previous experiment, we noted that minors appeared to follow a meandering route on trails. The aim of this experiment was to quantify this and to establish the proportions of transporting ants that were minors or had minors hitchhiking. The time taken for unladen ants to travel along a straight 20-cm length of trail, 1 m from the entrance hole, was recorded, together with the number of 45° turns made by the ant during this time. This was done for 70 foragers and 69 minors, with approximately equal numbers of incoming and outgoing ants. Five trails from different nests were used, all of which were flat and had been completely cleared of vegetation by the ants. Records with a similar purpose were made for a further 514 foragers and 454 minors, but recording instead whether the ant wandered to the point of contacting the edge of the trail. These records were made on seven trails from different nests. Finally, using ten trails from different nests, we recorded whether transporting workers were minors or foragers (n=715), and if the ants had minor workers hitchhiking on the pieces of grass being carried (n=380).

The time taken and number of turns made by minor workers and foragers were compared using unpaired t-tests. In the second part of the experiment, the proportions of minor workers and foragers that wandered to the edge of the trail were compared with a G-test, with G adjusted by William's correction factor.

Effect of context on the alarm response

The aggressiveness of many social insects is related to distance from the nest and the level of activity (Shorey 1973), and leaf-cutting ant trails vary in activity over the foraging period. The aim of this experiment was to test whether the alarm response was affected by distance from the nest (10 cm, 1 m or 5 m), time of day (0730–1030 hours versus 1530–1900 hours) and trail activity (high or low). High-activity trails had more than 25 ants per minute passing a point 1 m from the entrance hole, and low-activity trails had fewer than this. Tests comparing the times of day or the activity levels were carried out at the 1-m position. In all cases, crushed ant heads were used as the alarm sources and were placed 5 cm to the side of the trails in the centre of 10-cm-diameter circles cleared of vegetation. Each context was replicated 20 times using 20 different trails.

A 1-min count of the number of ants travelling along the trail was made immediately prior to the experiment at the point on the trail adjacent to where the source was to be placed. At 2 min after application of the crushed head, a near-instantaneous count was made of the number of ants within the 10-cm-diameter circle. This was also done prior to application, but at this time, virtually no ants were recorded in any of the circles and these data was not analysed further. Ants counted in both the trail traffic and circle counts were recorded as being either minors or foragers, and as either transporting or unladen.

The data were log or log (x+1) transformed, and the contexts compared with either a one-way factorial ANOVA or unpaired t-tests. G-tests were used to compare the proportions of minor workers to foragers, and the proportions of foragers that were transporting. The "proportions responding" were calculated as the ratios of ants in the circles to ants in the trail traffic, and these proportions were also compared with G-tests. G was adjusted with William's correction factor where there was only 1 df.

Results

Polyethism in the alarm reaction

The alarm sources resulted in significant increases in both the traffic of ants along the roads ($F_{6,81}$=10.9, P<0.001) and the number of ants within the test areas ($F_{6,81}$=10.32, P<0.001). Very few ants were ever associated with the controls. Although more ants responded to whole ants than to crushed heads alone, the proportions of minor workers to foragers responding did not differ between the treatments and so the data were combined. Following application of the alarm sources, the proportion of ants on the roads that were minor workers increased considerably (Fig. 2). The proportion of ants that were minors on the roads was the same as on the trails at time 0 (G_{adj}=0.01, df=1, P>0.05), but was significantly greater than on the trails at 2 min after application (G_{adj}=27.7, df=1, P<0.001). The proportion continued to increase to 82.1±6.1% at 10 min after application (G_{adj}=40.4, df=1, P<0.001). The proportion of ants that were minors within the test areas was also significantly higher than on the trails at 10 min after application of the sources (G_{adj}=78.0, df=1, P<0.001). However, neither the number of ants on the trails (treatment-time interaction: $F_{6,81}$=0.95, P=0.46; main effect of time: $F_{3,81}$=2.52, P=0.06), nor the proportion of them that were minor workers (treatment-time interaction: $F_{6,81}$=0.99, P=0.44; main effect of time: $F_{3,81}$=1.00, P=0.40) changed significantly in any of the treatments. Transporting ants never responded during the alarm reactions, and there was no effect of the treatments on the traffic of transporting workers along the trail (treatment-time interaction: $F_{6,81}$=1.11, P=0.36; main effect of time: $F_{3,81}$=0.09, P=0.97).

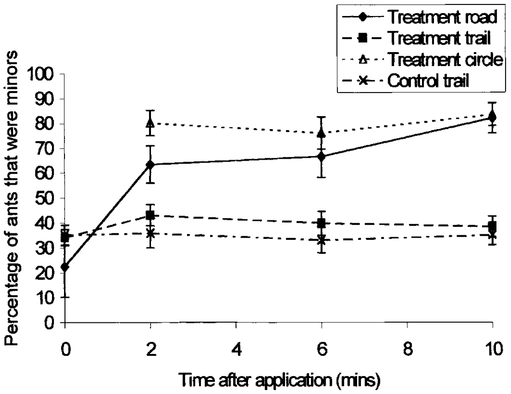

Fig. 2 Response of *Atta capiguara* to alarm sources. Mean (±SE) percentage of ants counted that were minor workers on the treatment trails, the treatment roads, in the treatment test areas and on the control trails. Data for the two treatments are combined. Insufficient ants were counted on the control roads or in the control test areas for meaningful interpretation

Trail behaviour

Foragers took 9.3±0.7 s to travel the 20-cm distance, while minors took 24.3±2.9 s (t=5.05, df=137, P<0.001). This difference was only partly due to foragers being larger than minors (the fastest times recorded were 3.4 s for foragers and 4.1 s for minors) and appeared to be largely a result of the minor workers following a more meandering path. Minor workers made significantly more 45° turns than foragers [8.8±1.3 (minors) vs 1.1±0.3 (foragers); t=5.64, df=137, P<0.001]. They frequently back-tracked, and on some occasions never trav-

Table 1 Results of the third experiment examining the effect of context on the alarm response

Context		Trail traffic			Ants responding	
		Number of ants	Percentage of ants transporting grass	Percentage of ants that were minor workers	Number of ants	Percentage of ants that were minor workers
Position	10 cm	67.0±6.9	37.8±3.6	29.3±4.3	22.3±3.4	63.9±4.6
	1 m	50.2±4.8	34.2±3.6	27.4±2.8	18.6±3.2	55.3±5.6
	5 m	38.9±5.9	40.6±5.1	13.7±3.2	9.4±2.3	45.9±6.9
	Significance	$F_{2,57}=6.63$, $P=0.003$	$G=17.0$, $df=2$, $P<0.001$	$G=90.8$, $df=2$, $P<0.001$	$F_{2,57}=5.96$, $P=0.004$	$G=3.0$, $df=2$, $P>0.05$
Time	Morning	32.6±6.1	16±3.4	23.4±3.8	15.9±3.1	54.6±6.5
	Afternoon	29.7±5.0	43.8±4.5	16.8±3.1	9.9±1.1	53.5±6.3
	Significance	$t=0.26$, $df=38$, $P=0.79$	$G_{adj}=107.2$, $df=1$, $P<0.001$	$G_{adj}=11.9$, $df=1$, $P<0.001$	$t=1.77$, $df=38$, $P=0.085$	$G_{adj}=2.37$, $df=1$, $P>0.05$
Activity	High	50.2±4.8	31.4±5.8	24.9±3.4	18.6±3.2	65.3±5.6
	Low	12.1±1.0	28.4±4.3	15.3±3.3	7.3±1.1	43.4±6.2
	Significance	$t=10.4$, $df=38$, $P<0.001$	$G_{adj}=0.23$, $df=1$, $P>0.05$	$G_{adj}=8.9$, $df=1$, $P<0.01$	$t=2.7$, $df=38$, $P=0.009$	$G_{adj}=25.2$, $df=1$, $P<0.001$

elled the full 20-cm distance, instead returning the way they had come. Foragers almost always followed the trail in the same direction. In the second part of the experiment, 17.8% of the minor workers wandered to such a degree that they contacted the trail edge, while only 6.8% of the foragers did ($G=28.1$, $df=1$, $P<0.001$). Of the transporting workers, only 0.98% ($n=715$) were minor workers and only 2.1% ($n=380$) had minor workers hitchhiking.

Effect of context on the alarm response

Crushed heads placed 10 cm from the entrance elicited the largest response, with a slightly lower response at 1 m from the entrance (Table 1). Although ants still responded in an aggressive manner when the crushed heads were placed 5 m from the trail entrance, the number of ants responding was considerably lower. This did not appear to be related to the trail traffic, because the main decrease in traffic occurred between 10 cm and 1 m, and the proportion of ants responding relative to the trail traffic also differed significantly between the positions ($G=19.1$, $df=2$, $P<0.001$). However, the decrease in response did correspond to the proportion of the trail traffic that was made up of minor workers. This decreased as distance from the trail entrance increased, with the main decrease being between 1 and 5 m (Table 1).

Although there was no significant difference between the morning and afternoon periods in the number of responding ants (Table 1), the proportions responding relative to the trail traffic did differ significantly, with a greater proportion responding during the morning period ($G_{adj}=12.7$, $df=1$, $P<0.001$). A greater proportion of the trail traffic was minor workers at this time, and a lower proportion of the foragers were transporting grass loads (Table 1).

Far fewer ants responded when crushed heads were applied by low-activity compared with high-activity trails (Table 1). Of more interest, the proportions responding relative to the trail traffic were significantly greater on the low-activity trails ($G_{adj}=14.4$, $df=1$, $P<0.001$). Yet there was no difference between the two activity levels in the proportion of foragers transporting, and the ratio of minors to foragers in the trail traffic was actually lower on the low-activity trails (Table 1).

Discussion

Transporting workers were not found to respond at all during the alarm reactions, in agreement with previous work by Moser et al. (1968), Crewe and Blum (1972), and Pow (1996). Interestingly, minor workers appeared to be most involved in the alarm reaction. Whereas 34.7±2.8% of the trail traffic consisted of minor workers in the first experiment, 82.1±6.1% of the ants that responded in the alarm reaction were minors. Although leaf-cutting ant soldiers are traditionally thought to be the colony's defenders, ants of all sizes will attack alien conspecifics (Wilson 1980a; Vilela and Howse 1986). Whitehouse and Jaffé (1996) found that most of the *A. laevigata* workers recruited to conspecific or interspecific ant threats were small (less than 5 mm long). Furthermore, minor and media workers of *A. laevigata* are more efficient than major workers or soldiers at recognising intruders (Salzemann and Jaffé 1991). Minors are also more sensitive than their larger nestmates to substrate-borne vibrations resulting from stridulation (Roces and Hölldobler 1995), which is another signal produced by alarmed ants (Markl 1965, 1967; Roces and Hölldobler 1995).

Many previous authors have noted the presence of large numbers of minor workers on leaf-cutting ant trails (Stradling 1978; Knapp 1995; Pow 1996), but the role of these ants is unclear. The function normally ascribed to ants on foraging trails is the cutting and transportation of vegetation. However, only 0.98% of the transporting workers on the *A. capiguara* trails in this study were minors. The main role suggested for minor workers on trails is the defence, by hitchhiking, of nestmates against parasitic phorid flies (Eibl-Eibesfeldt and Eibl-Eibesfeldt 1967; Feener and Moss 1990; Orr 1992). However, in the current study, only 2.1% of transporting workers had minors hitchhiking on their loads, despite minors making up a large proportion of the trail traffic, and phorid parasites were never observed. Protection against phorids therefore seems an insufficient explanation for the large numbers of minor workers found on the trails in this study.

The minor workers were found to be the main group to respond during the alarm reaction. They were also found to follow a slow, meandering route along the trail that was clearly different from the fast, purposeful paths taken by the larger foragers. A similar pattern has been observed in *Pogonomyrmex*. Gordon (1984, 1987, 1989) described a distinct extranidal class of workers called “patrollers”. They followed a characteristic, hesitant zigzag path along the trail, did not engage in any obvious task and were the main group to respond during alarm reactions. Patrollers have also been described in the ponerine *Paraponera clavata* (Nelson et al. 1991), and they again responded vigorously to disturbances. This behaviour is strikingly similar to that of *A. capiguara* minor workers on foraging trails. *A. capiguara* minors appear to be patrolling the area of the trail for threats, and they seem more likely than their larger nestmates to respond to threats. While such threats may include phorid parasites, the results suggest that leaf-cutting ant minor workers have a far more general role in the defence of trails than simply protecting against phorids.

Leaf-cutting ants have evolved a soldier caste specifically for defending the colony, so why do the minor workers play the main role in the alarm reaction on trails? Minors will certainly be less costly to produce than larger ants. Several further advantages suggest themselves. Having a greater number of individuals will increase the chances of discovering a threat (Adler and Gordon 1992) and the energetic cost per unit of information found is lower for smaller workers (López et al. 1997). In addition, using large numbers of smaller workers in the response may increase the chances of winning intercolony disputes (Whitehouse and Jaffé 1996), for the same reasons that army ants use large numbers of small workers to overcome their social insect prey (Franks and Partridge 1993). Soldiers normally remain within the nest (Moser 1967), and their function may be to defend the nest itself against vertebrate predators.

The context in which a stimulus is encountered can affect the response of ants, and in this study, both the positional and temporal context were important. Jutsum (1979) found that leaf-cutting ants were less aggressive further from their nest, but although the numbers responding did decrease, ants in our experiment continued to respond in a highly aggressive manner even 5 m from the trail entrance. The decrease in the proportion responding relative to the trail traffic appeared to be due to the proportionally fewer minor workers in the traffic further along the trail. Similarly, the proportion responding relative to the trail traffic was greater in the morning period, when the proportion of trail traffic that was minor workers was higher. Fewer foragers transported grass in the morning period, and as transporting workers did not respond during these experiments, this would have further increased the number of ants available to respond during an alarm reaction.

The difference in response between the two activity levels was particularly interesting. The proportion responding relative to the trail traffic was higher on low-activity trails. Yet the proportion of foragers that were transporting did not differ between activity levels, and the proportion of minors in the trail traffic was lower on low-activity trails. Ants travel more slowly along a less well marked trail (Beckers et al. 1992), and the pheromone plume emitted from a point source is discontinuous (Murlis et al. 1992). Thus, fast-moving ants on a well-marked trail may be less likely to respond simply because they are less likely to encounter a pheromone filament. Minor workers move more slowly along trails, which may explain why they are more likely to respond than their larger, faster-moving nestmates. Ants are also less motivated to follow trails that are less well marked (Jaffé and Howse 1979), so another possibility is that ants have a lower response threshold to alarm pheromone when on the less well marked low-activity trails.

A final point of interest is that the seemingly unoccupied minor workers responded, while the clearly occupied transporting workers did not. This suggests that the most important factor governing whether or not an ant responds in an alarm reaction may be the degree to which the individual is already engaged in a task; unengaged workers will respond more readily than those already occupied. In both *Novomessor* (Markl and Hölldobler 1978) and *Pogonomyrmex* (Gordon 1987), unoccupied workers have been found to be more responsive than those engaged in a task such as food transport. A division of labour such as this will obviously be more efficient for the group as a whole, providing there are normally sufficient unoccupied workers available to respond to the threat.

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