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Vibrational communication between hitchhikers and foragers in leaf-cutting ants (*Atta cephalotes*)

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Abstract In a foraging column of the leaf-cutting ant *Atta cephalotes*, minim workers (the smallest worker subcaste) “hitchhike” on leaf fragments carried by larger workers. It has been demonstrated that they defend leaf carriers against parasitic phorid flies. The present study examines the cues used by the potential hitchhikers to locate leaf carriers. As recently reported, foraging workers stridulate while cutting a leaf fragment, and the stridulatory vibrations serve as close-range recruitment signals. We tested the hypothesis that these plant-borne stridulatory vibrations are used by the potential hitchhikers to locate workers engaged in cutting. Three different lines of evidence support this view. Firstly, the repetition rate of the stridulations produced by foraging workers increases significantly as foragers maneuver the leaf fragment into the carrying position and walk loaded to the nest. This is the moment when hitchhikers usually climb on the leaf. Although the leaf-borne stridulatory vibrations are considerably attenuated when transmitted through the workers’ legs, they can nevertheless be detected at short distances by minims. This subcaste is several times more sensitive to substrate-borne vibrations than larger workers. Secondly, when a “stridulating” and a “silent” leaf were simultaneously presented at the foraging site, minim workers spent significantly more time on the stridulating than on the silent leaf. Thirdly, hitchhiking was more frequent in leaf carriers which cut fragments out of the stridulating leaf than in those cutting the silent leaf.

Key words Leaf-cutting ants · *Atta cephalotes* · Foraging · Stridulation · Parasitism

Introduction

Division of labor among workers in social insect colonies continues to be of considerable interest, and recently many attempts have been made to understand both its physiological basis and the integration of individual workers into colony function (reviewed in Gordon 1989; Hölldobler and Wilson 1990). Together with division of labor by age (temporal polyethism), almost universal in social insects, some species show division of labor based on physical castes (alloethism). Among the Formicidae, leaf-cutting ants are one of the most polymorphic species: a single colony may contain workers that span a 200-fold range in body mass (Weber 1972). This remarkable polymorphism is the basis for an elaborate alloethism: different tasks are performed by workers of different size (Wilson 1980a, b).

Division of labor in leaf-cutting ants can also be observed during foraging. For instance, not all workers in a foraging column carry leaf fragments: between 13 and 75% of them return to the nest unladen (Hodgson 1955; Cherrett 1972; Lugo et al. 1973; Lewis et al. 1974). It has been shown that a number of these unladen ants can be involved in trail clearing (Daguerre 1945), transport of plant sap (Stradling 1978), or reinforcement of the chemical trail (Jaffé and Howse 1979; Roces and Hölldobler 1994).

Minim workers (the smallest worker subcaste) can also be seen among foraging workers, even though they are unable to cut leaf fragments (Wilson 1980a). At the host plant, they usually walk around the cutting sites, or stand with their mandibles opened and their antennae outstretched near workers engaged in cutting. At the cutting site and also along the foraging trail they often investigate leaf carriers by briefly climbing onto the carrier and its leaf fragment. In fact, many of them do not walk back to the nest, but ride (“hitchhike”) on the leaf fragments being carried to the nest. It has been demonstrated that they defend leaf carriers from

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attacks by parasitic phorid flies, which attempt to oviposit on the ants' bodies (Eibl-Eibesfeldt and Eibl-Eibesfeldt 1967; Feener and Moss 1990).

The present study examines the cues used by the potential hitchhikers to locate leaf carriers, in the leaf-cutting ant *Atta cephalotes*. In a previous study, we reported that foraging workers stridulate while cutting a leaf fragment, and that the stridulatory vibrations are transmitted into the substrate through the worker's head. Workers respond to the vibrations transmitted through the plant material by orienting toward the source of the vibrations. We therefore concluded that stridulatory vibrations act as close-range food-recruitment signals (Roces et al. 1993). Here we investigate whether these plant-borne stridulatory vibrations are also used by potential hitchhikers to locate workers engaged in cutting leaves. We first recorded the repetition rate of the stridulations produced by foragers during their cutting activity, and compared it with the repetition rate recorded in the same workers at the moment when hitchhiking usually occurs, i.e., as foragers maneuver the leaf fragment into the carrying position and walk loaded to the nest (Eibl-Eibesfeldt and Eibl-Eibesfeldt 1967; Feener and Moss 1990). We also compared the behavior of minim workers when they were presented with an artificially "stridulating" and a "silent" leaf.

Methods

The study was carried out with a laboratory colony of *A. cephalotes* collected near La Selva, Heredia Province, Costa Rica. At the time of the experiments, the colony was approximately 4 years old, and its fungus garden occupied a volume of c. 9 l. During the experimental period the colony was fed primarily with leaves of privet (*Ligustrum vulgaris*).

Repetition rate of stridulations by foraging workers during their cutting activity, and during walking with the load

The repetition rate of the stridulatory vibrations produced by an individual worker while cutting a leaf fragment, and as it walked with its load, was measured using non-invasive laser Doppler vibrometry (Michelsen and Larsen 1978). The basic methodology is described by Roces et al. 1993, and can be briefly summarized as follows. Firstly, we offered several leaves of *Prunus laurocerasus* (Rosaceae) individually pinned to the foraging table. When a worker started to cut at the leaf edge, we carefully removed the leaf from the nest table and pinned it (through the mid-vein) vertically on a cork mounted on a vibration-buffered table, avoiding direct contact between leaf and substrate. Throughout this procedure, the ant continued undisturbed with its cutting behavior. We then focused the laser beam on a small white spot (2 mm diameter), painted on the leaf c. 2 cm away from the cutting site, and measurements of the plant-borne vibrations began.

As reported in our previous study (Roces et al. 1993), workers continued to stridulate as they maneuvered the leaf fragment into the carrying position and walked with their loads to the nest. Maneuvering of the leaf fragment always occurred at the cutting site. During these procedures, the stridulatory vibrations were led

into the substrate (leaf) through the worker's legs. These vibrations could easily be recorded at the same point where the laser beam was focused during the ant's cutting activity.

The stridulatory vibrations produced by a loaded worker during walking are transmitted into the substrate through the workers' legs. In order to record them, we had to continuously focus the laser beam on a moving reflecting surface as the worker was running with its load to the nest. This proved to be extremely difficult. To obtain reliable measurements of stridulations during walking, we took advantage of the following observation: in our experimental arrangement, loaded workers could not return directly to the nest, and therefore continued to walk on the vertically-pinned leaf for approximately 1 or 2 min. This made it possible for us to record leaf-borne stridulatory vibrations at a fixed measuring point.

We analyzed the records using the computer program Spike2 (Cambridge Electronic Design, 1992), and counted in different workers the number of stridulations produced 2 min before and 1 min after the completion of the cut. Next, we calculated the signal repetition rate per second, both during and after the cutting activity. Statistical comparisons were made using a one-way ANOVA test.

Stridulatory vibrations and occurrence of hitchhikers

To analyze the possible role of plant-borne stridulations as communication signals between hitchhikers and foraging workers, we presented one "stridulating" and one "silent" leaf of *P. laurocerasus* simultaneously on the foraging table. When a foraging column was established, we compared the behavior of the minims walking on the vibrating and silent leaves, and recorded the actual occurrence of hitchhikers.

Each assay was initiated by presenting a patch of privet leaves on the foraging table (a plastic box measuring 18 × 18 × 9 cm) for 15 min, in order to increase the number of workers actually engaged in foraging. Subsequently, we replaced these leaves with two large leaves of *P. laurocerasus* [approximately 12 cm long, mean leaf density (leaf mass/area) = 0.39 mg/mm²]. In order to simulate a "stridulating" leaf, we first glued the ventral side of each leaf to one end of a 6 cm-long metal rod (3 mm in diameter), inserted through a hole on the foraging table. In this way, both leaves were elevated 3 mm above the table surface, and placed next to each other, separated by a 3-mm gap. Only the tip of each leaf contacted the floor. Beneath the table, each rod was connected with a separate vibrator (Brüel-Kjaer model 4810), through which we continuously played back stridulatory vibrations previously recorded in foraging workers. A switch allowed a change between the stridulating and the silent side. The signals consisted of chirps repeated at a rate of 15–20 per second, each chirp resulting from the impact of the scraper on the file during the upward movement of the gaster, as previously described by Markl (1968). A sequence of the stridulatory vibrations played back on the *P. laurocerasus* leaf is presented in Fig. 1. The velocity of the leaf's vibrations during each chirp (approximately 4 mm/s peak/peak) corresponds with values reported in a previous study (Roces et al. 1993).

The behavior of the ants on the leaves was videotaped until the first ten leaf fragments had been cut from the one or the other leaf. At this point we also counted the number of fragments cut out of the other leaf to see whether the ants preferred the vibrating or the silent leaf. We performed a total of 15 assays, each lasting approximately 15–20 min, no more than three per day. For each test we changed the stridulating and the silent side in order to cancel any side preference.

During the analysis of the videotapes, the number of minim workers observed per assay was small, and we were able to follow them individually as they walked on a given leaf. In this way, we recorded the following variables:

1. The time spent by each observed minim worker on either the "stridulating" or the silent leaf.

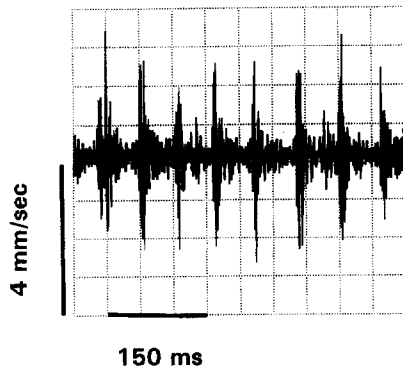


Fig. 1 Record of the leaf-borne stridulations played back during the experiments, showing eight individual "chirps" (stridulations) repeated at a rate of approximately 18 s^{-1} . Signals were recorded on the leaf surface via laser-Doppler-vibrometry. Velocity of the leaf's vibration (c. 4 mm/s peak/peak) corresponds with values previously reported (Roces et al. 1993)

2. The number of minim workers observed on each leaf during the total duration of the assay.

3. The occurrence of hitchhiking in leaf carriers returning from the stridulating or the silent leaf.

In order to investigate whether artificial stridulations modulate the responses of workers actually engaged in cutting, we also quantified the percentage of workers that stridulated while cutting leaf fragments, in both the stridulating and the silent leaf. The counts were performed directly during the assays, without need to record the vibrations produced, since the gaster's movements are conspicuous enough to be clearly recognized.

As we could not exclude the possibility that some workers cutting the "silent" leaf may also stridulate, we have to take into account that the non-vibrating leaf was not completely silent. In order to eliminate stridulations on the silent leaf completely, we performed an additional series of experiments using large *P. laurocerasus* leaves of high toughness (mean leaf density = 0.55 mg/mm^2). Such tough leaves proved not to be attractive to the ants, and no foraging workers were observed to initiate cutting during the experiment. The absence of foragers actually engaged in leaf-cutting ensures that any preference of the minim workers for the vibrating or silent leaf is entirely due to the presence (or absence) of the stridulatory vibrations played back. A total of ten assays were performed.

After the experiments, we took a sample of minim and foraging workers and weighed them to the nearest 0.1 mg , in order to obtain a quantitative figure of worker polymorphism.

Results

Signal repetition rate

Figure 2 depicts the repetition rate of the stridulatory vibrations produced by individual workers both during their cutting activity and as they maneuvered the fragment into the carrying position and walked with their loads. Workers that had just finished cutting a leaf fragment significantly increased the repetition rate of the stridulation signals (one-way ANOVA test, $F = 124.7$, $P < 0.0001$). Even workers which did not stridulate during cutting were observed to stridulate as they loaded up the fragment (example in Fig. 2, ant num-

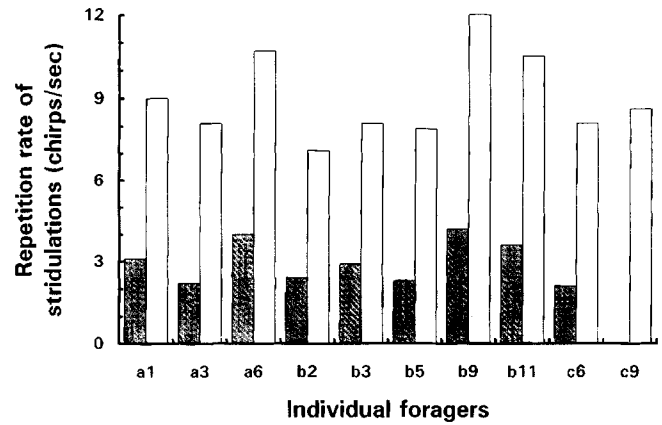


Fig. 2 Mean repetition rate of stridulatory vibrations (chirps per second) produced by individual workers of *Atta cephalotes*. Shaded bars: stridulations produced while cutting a leaf fragment (average during the last two minutes prior to the completion of the cut). Open bars: stridulations while maneuvering the leaf into the carrying position and walking on the leaf with the load (average over 1 min). Standard error (not shown) ranged from ± 5 to 13% . Data from a random sample of workers, out of a total of 20 foragers

ber c9). These leaf-borne vibrations were transmitted through the workers' legs. They showed considerable attenuation in comparison with those transmitted mostly through the mandibles, when workers are actually engaged in cutting (see Rocés et al. 1993). Their amplitudes averaged $2 \times 10^{-6} \text{ cm}$, and were 4–5 times lower than those of the stridulations recorded during the cutting activity. As a result, 2–3 cm away from the stridulating worker, the leg-transmitted stridulations were indistinguishable from noise in the laser-vibrometer recordings.

It should be mentioned that this increase in the signal repetition rate after the completion of the cut is unlikely to be the result of the experimental manipulations, because it was also observed in other circumstances. We videotaped workers as they finished their cutting activity, and proceeded carrying the leaf fragments to the nest. During walking, loaded workers also showed the typical stridulatory movements (raising and lowering of the gaster) at a high repetition rate as presented in Fig. 1.

Stridulatory vibrations and the occurrence of hitchhikers

In our study, minim workers averaged $1.3 \pm 0.4 \text{ mg}$ ($n = 22$), while leaf carriers weighed $5.9 \pm 1.6 \text{ mg}$ ($n = 27$). The behavioral responses observed when we presented at the foraging table a stridulating and a silent leaf are summarized in Table 1. The mean number of minim workers observed on the leaf per assay, i.e., the number of potential hitchhikers, was similar for both the stridulating and the silent leaf (Table 1, first row). However, minim workers were observed to remain significantly longer on the stridulating than on the

Table 1 Number and behavioral responses of minim workers ("hitchhikers") and leaf carriers of the leaf-cutting ant *Atta cephalotes* recorded on an artificially-"stridulating" or a "silent" (control) leaf of *Prunus laurocerasus* (mean \pm S.D.). A total of 15 assays were performed. G_{adj} value from independence G -test, after Williams' correction; χ^2 value from chi-square contingency analysis. Level of significance: $\alpha = 0.01$

	"Stridulating" leaf	"Silent" leaf	Statistic	<i>P</i>
Mean number of potential hitchhikers observed on the leaf per assay	3.2 \pm 1.1 (<i>n</i> = 15)	2.9 \pm 0.9 (<i>n</i> = 15)	<i>t</i> = 0.81	NS
Mean time spent by the potential hitchhikers on the leaf (min)	2.02 \pm 1.43 (<i>n</i> = 48)	1.08 \pm 0.76 (<i>n</i> = 43)	<i>t</i> = 3.85	<0.001
Number of fragments cut per assay	9.0 \pm 1.1 (<i>n</i> = 15)	8.8 \pm 1.6 (<i>n</i> = 15)	<i>t</i> = 0.39	NS
Number of leaf carriers with hitchhikers/total number of leaf carriers	12/135 (8.9%)	2/132 (1.5%)	$G_{adj} = 7.80$	<0.01
Percentage of workers that stridulated while cutting	54.8% (<i>n</i> = 135)	50.0% (<i>n</i> = 132)	$\chi^2 = 0.62$	NS

Table 2 Time spent by minim workers (potential hitchhikers) of the leaf-cutting ant *A. cephalotes* on an artificially-"stridulating" or a "silent" (control) leaf of *P. laurocerasus* presented at the foraging table (mean \pm SD). Leaves presented were of high toughness [mean leaf density (leaf mass/area) = 0.55 mg/mm²], so that no foraging workers were observed to cut fragments. A total of ten assays were performed

	"Stridulating" leaf	"Silent" leaf	Statistic	<i>P</i>
Mean number of potential hitchhikers observed on the leaf per assay	4.2 \pm 1.9 (<i>n</i> = 10)	4.9 \pm 2.1 (<i>n</i> = 10)	<i>t</i> = 0.78	NS
Mean time spent by the potential hitchhikers on the leaf (min)	1.63 \pm 1.17 (<i>n</i> = 42)	0.90 \pm 0.89 (<i>n</i> = 49)	<i>t</i> = 3.38	<0.001

silent leaf (Table 1, second row). It is important to mention that if minim workers remained for shorter periods on the silent leaf, and if the probability of finding either of the two leaves is roughly similar, the total number of minims counted on the silent leaf during the entire assay should be greater than on the stridulating leaf. This was not the case, because not all minim workers leaving a leaf subsequently mounted the other one. Instead, they were observed walking around the table.

The stridulatory vibrations played back on the leaf did not result in an increase of the number of leaf fragments cut by foraging workers (Table 1, third row). However, the occurrence of hitchhikers was significantly higher in leaf carriers that cut fragments out of the stridulating leaf than in those cutting the silent leaf (Table 1, fourth row). When hitchhiking occurred, the actual number of minim workers transported by one leaf carrier was always one. However, in the field one can often observe more than one hitchhiker on a leaf fragment being carried (Fig. 3; see Feener and Moss 1990). It is worth mentioning that under our experimental conditions, laden foragers reached the nest promptly by covering a distance of only 15 cm. As a result, it was impossible to determine whether there is a negative feedback on signal production, i.e., whether the presence of a minim on the carried leaf fragment causes a forager to reduce the rate and/or the intensity of its stridulatory vibrations.

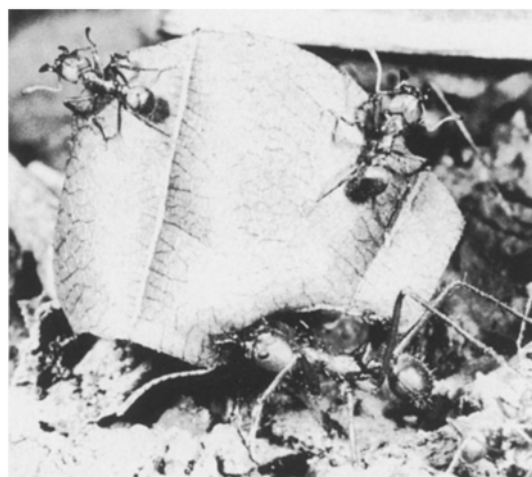


Fig. 3 Minim workers of *A. cephalotes* hitchhiking on a fragment carried by a forager along a field foraging column

The percentage of workers that stridulated while cutting leaf fragments averaged roughly 50%, and was similar for both the stridulating and the silent leaf (Table 1, fifth row). The observation of stridulation by workers cutting the silent leaf indicated that it also vibrated as long as some workers were cutting it, though not as uninterruptedly as the stridulating leaf.

Even in the absence of workers actually engaged in leaf-cutting, the potential hitchhikers spent longer on

the stridulating leaf than on the silent one (Table 2), i.e., minims were halted by the stridulatory vibrations alone, without the need of physical contact with leaf-cutting workers. In addition, the presence of workers engaged in cutting did not result in longer times being spent by minim workers on the leaves, neither on the stridulating (comparison between mean time values from Table 1 and Table 2, $t = 1.40$; $P > 0.1$; NS), nor on the silent leaf ($t = 1.02$; $P > 0.2$; NS).

Discussion

It is well documented that minim workers of leaf-cutting ants of the genus *Atta* often ride on the leaf fragments being carried by large workers (Eibl-Eibesfeldt and Eibl-Eibesfeldt 1967; Feener and Moss 1990; Orr 1992). These hitchhikers protect the leaf carriers from attacks by parasitic phorid flies. Three different lines of evidence support the idea that hitchhikers and leaf carriers communicate by using plant-borne stridulatory vibrations produced by the carriers.

Firstly, the significant increase in the repetition rate of the stridulations produced by foraging workers as they maneuvered the leaf fragment into the carrying position and returned laden to the nest. Even workers which did not stridulate during cutting were observed to stridulate as they loaded up the fragment. This is the moment when hitchhiking usually commences, even though it is a dynamic process which is also observed along foraging trails (Feener and Moss 1990). The leaf-borne vibrations, transmitted through the workers' legs, were considerably attenuated, as recently reported (Roces et al. 1993). Their amplitude, c. 2×10^{-6} cm, lies near the sensitivity threshold measured electrophysiologically in leg nerves of *Atta* workers (1.3×10^{-7} cm in forelegs of minor workers, Markl 1970), which make possible the detection of the signals up to a maximum distance of 2–3 cm. Even though stridulatory vibrations serve to orient workers to the foraging site (Roces et al. 1993), it is unlikely that the vibrations transmitted through the workers' legs can be used as recruitment signals, because of their relatively short transmission distance. They are expected to be effective only in the immediate vicinity of the stridulating worker. Non-riding minim workers usually walk around the cutting site or approach leaf-carriers that are harassed by parasitoids along the trails, and then climb on their leaf fragments. Feener and Moss (1990) suggested that leaf carriers attract minims along the trail because they stop and disrupt the flow of traffic when they are harassed by phorid flies. Our results suggest that the stridulatory vibrations produced by leaf carriers are also important communication signals. The high attenuation of the signal does not preclude its use as orientation cue, because minims are on average 3–4 times more sensitive to substrate-borne vibrations than

large workers (Markl 1970), and they may be close enough to perceive them.

Secondly, the leaf-borne stridulatory vibrations proved to be highly attractive for minim workers. They spent significantly longer on the "stridulating" than on the "silent" leaf, even in the absence of cutting workers (Tables 1 and 2).

Thirdly, the occurrence of hitchhikers was significantly higher in leaf carriers foraging on continuously stridulating leaves, even though the number of leaf carriers was roughly similar for both the stridulating and the silent leaf (Table 1, third row). Thus, the increased occurrence of hitchhiking is not the result of a higher number of loaded workers being contacted by the minims. It is important to note that in our experiments, the non-vibrating leaf was called silent. However, since 50% of workers cutting fragments actually stridulated, the leaf was not completely silent. Hitchhiking was also observed on this silent leaf, but less frequently. Since the number of available leaf carriers was similar for both kinds of leaves, we suggest that the perception of stridulatory vibrations increased the readiness of the minims to respond by climbing on a leaf carrier (Table 1).

Since stridulatory vibrations serve as orientation signals for foraging workers during recruitment (Roces et al. 1993), we had expected that the artificially-stridulating leaf should be more attractive than the silent one. However, the number of both minims walking on the leaves and foragers engaged in cutting was similar, irrespective of the presence of stridulations. A probable explanation is that in the small foraging arena used, workers were able to quickly find the large leaves, without the need to use vibrations as orientation signals.

As in several previous field studies (Cherrett 1968, 1972; Lewis et al. 1974), we recorded a relatively small occurrence of hitchhikers, between 1.5 and 8.9% of the total number of laden foragers returning to the nest. Interestingly, results of field experiments indicate that leaf-cutting ants adjust the level of hitchhiking to accommodate both daily and seasonal changes in the abundance of parasitic phorid flies (Feener and Moss 1990). In our study, the level of hitchhiking was increased upon the perception of more frequent stridulatory vibrations. It is an open question whether the higher level of hitchhiking observed in the field is due to increased hitchhiking activity of minims because of the detection of parasites, an increase in the number of foragers that stridulate because they were attacked and attempt to attract potential hitchhikers, or a combination of these possibilities. It is important to mention that while members of a number of phorid fly species attack laden foragers along the trail, others parasitize only unladen ants (reviewed by Feener and Moss 1990). Eibl-Eibesfeldt and Eibl-Eibesfeldt (1967) observed that upon attack, workers actually engaged in cutting leaves defend themselves by stretching their hind legs upward to chase off the flies, while continuing

with the cutting activity. In this line of arguments, it is hypothesized that the attacked foragers stridulate as an alarm reaction, as several stridulating ant species do (Markl 1973; Hölldobler and Wilson 1990). If so, one might expect that in the presence of flies foragers would increase either the rate or the intensity (or both) of their stridulatory vibrations, in order to attract minims for defense. We were unable to simulate this situation under our laboratory conditions, so that the link between parasite presence and production of stridulation by foragers remains to be investigated under field conditions.

Although ant stridulation occurs in a variety of contexts (Hölldobler and Wilson 1990), few effects of these signals have been clearly demonstrated. It plays a role in underground alarm communication (Markl 1965), mating (Markl et al. 1977), recruitment to food sources (Markl and Hölldobler 1978; Hahn and Maschwitz 1985; Baroni-Urbani et al. 1988; Roces et al. 1993), and during leaf-cutting (Tautz et al. 1995). Our present results demonstrate an additional function of stridulatory vibrations in ants, i.e., communication between castes in the context of defense against parasites, and further support the idea that the effects of stridulatory vibrations, despite their elementary and unitary character, depend on the social context where they are perceived (Roces et al. 1993).

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