RESCUE BEHAVIOUR SHOWN BY WORKERS OF *FORMICA SANGUINEA* LATR., *F. FUSCA* L. AND *F. CINEREA* MAYR (HYMENOPTERA: FORMICIDAE) IN RESPONSE TO THEIR NESTMATES CAUGHT BY AN ANT LION LARVA

Wojciech Czechowski[1], Ewa Joanna Godzińska[2] and Marek W. Kozłowski[3]

[1]*Laboratory of Social and Myrmecophilous Insects, Museum and Institute of Zoology, Polish Academy of Sciences, Wileza St. 64, 00-679 Warszawa, Poland; e-mail: wcz@miiz.waw.pl*
[2]*Laboratory of Ethology, Department of Neurophysiology, Nencki Institute of Experimental Biology, Polish Academy of Sciences, Pasteur St. 3, 02-093 Warszawa, Poland; e-mail: ejg@nencki.gov.pl*
[3]*Department of Applied Entomology, Warsaw Agricultural University, Nowoursynowska St. 166, 02-787 Warszawa, Poland; e-mail: kozlowski@alpha.sggw.waw.pl*

Abstract.— We report the results of field observations and experiments demonstrating that workers of *Formica sanguinea* Latr. and *F. cinerea* Mayr caught by a larva of an ant lion (*Myrmeleon formicarius* L.) can induce rescue behaviour in their nestmates. Typical rescue behaviour involves both the attempts to pull away the attacked ant by tugging at its limbs, and rapid, intense digging behaviour. In natural mixed colonies of *F. sanguinea* and *F. fusca* L., enslaved *F. fusca* workers display rescue behaviour when their heterospecific nestmate is caught by an ant lion larva. On the other hand, we did not observe nestmate rescue behaviour in monospecific *F. fusca* colonies. These data suggest that workers of *F. sanguinea* and *F. cinerea* caught by an ant lion emit some signals which summon their nestmates to arrive at their rescue. Workers of *F. fusca* either do not emit such signals, or their danger signals fail to elicit rescue behaviour in other ants. Expression of rescue behaviour in the studied ant species is discussed in the context of their life strategies, of their position in the interspecific competitive hierarchy, and of our knowledge about nestmate rescue behaviour, and signals eliciting alarm and digging behaviour in ants.

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Key words.— Ants, *Formica sanguinea*, *Formica fusca*, *Formica cinerea*, mixed colonies, social parasitism, slavery, cross-specific communication, co-operation, ant lions, *Myrmeleon formicarius*.

INTRODUCTION

The research devoted to co-operative behaviour of social insects provided examples of some of the most remarkable abilities for co-operation observed in the whole animal kingdom. The most striking forms of co-operative behaviour described in the ants include, among others, co-operative nest building, various techniques of collective hunting and group transport of prey and many sophisticated forms of nestmate recruitment (Hölldobler and Wilson 1990).

Our present study reports the results of field observations and experiments in which we analysed a particularly remarkable example of ant co-operative behaviour: nestmate rescue from a life-threatening situation.

Our present data demonstrate that workers of *Formica sanguinea* Latr. and *F. cinerea* Mayr (but not of *F. fusca* L.) captured by a larva of an ant lion (*Myrmeleon formicarius* L.) can induce a very characteristic pattern of rescue behaviour in their nestmates, including enslaved workers of *F. fusca* L. inhabiting natural mixed colonies of *F. sanguinea* and *F. fusca*.

Our present research started from an accidental observation made in Puszcza Białowieska (Białowieża Forest; NE Poland) in 1992 (Czechowski 1997). At the start of that observation, a worker of *F. sanguinea* fell into a pit of an ant lion larva situated at about 1 m from its nest. The capture of that ant by the ant lion was followed by an immediate response of its nestmates present nearby. Very rapidly about 10 workers converged on

the ant lion pit and initiated a rescue operation. Their rescue behaviour consisted in the attempts to pull the victim out of the pit by pulling at its antennae and legs, and in the attempts to attack the ant lion. The ants also displayed rapid and intense digging behaviour, brushing away with their mandibles and their forelegs the sand covering the ant lion and its victim. A single enslaved worker of *F. fusca* L. which accompanied the workers of *F. sanguinea* in that rescue operation behaved in exactly the same way as its heterospecific nestmates. As a consequence of that attack, the confused ant lion dropped its victim and started to pounce on the ants running across its pit. Each time the ant lion seized a *F. sanguinea* individual, the aggressiveness of the other ants increased, and, conversely, the level of their aggressiveness showed a visible decrease each time the victim was released by the ant lion. Interestingly, that rescue behaviour was induced only by captured workers of *F. sanguinea*. When at last the ant lion captured the worker of *F. fusca*, aggressive behaviour of *F. sanguinea* stopped abruptly. The ants calmed down and returned to their nest, leaving the slave to its fate.

That preliminary observation suggested strongly (1) that workers of *F. sanguinea* captured by an ant lion emit some signals able to induce rescue behaviour in their nestmates, (2) that these signals may trigger rescue behaviour not only in their conspecific nestmates, but also in enslaved workers of *F. fusca*, and, lastly, (3) that workers of *F. fusca* either do not emit such signals, or their danger signals do not elicit rescue behaviour in workers of *F. sanguinea*.

The aim of the present study was to throw more light of the validity of these preliminary conclusions. We report further observations of behaviour of workers of *F. sanguinea* and *F. fusca* during their encounters with ant lion larvae which have captured their homo- and heterospecific nestmates. Some of these encounters were observed by us in the field, others have been provoked experimentally. We also provide a detailed description of rescue behaviour of workers of yet another ant species, *F. cinerea* Mayr.

MATERIALS AND METHODS

The majority of the data reported in the present study was recorded during the field research carried out in a complex of sandy dunes overgrown with pine forest near Tvärminne (Hanko Peninsula, S Finland) in the years 1998–2001. About 30 ant species cohabit that dune complex (Gallé 1991; see also Czechowski 1999, 2000, 2001, Czechowski and Vepsäläinen 2001). The most frequent species include the three species discussed in this study: *F. sanguinea*, *F. fusca* and *F. cinerea*.

F. (Raptiformica) sanguinea Latr. (the blood-red ant) is a species of successional forest habitats. That species is a facultative slave-maker that raids species of the subgenus *Serviformica* For. *F. sanguinea* are aggressive territorial ants, and during their raiding period they do not respect the boundaries of territories of other ant species (see Czechowski 2000, Czechowski and Vepsäläinen 2001).

F. (Serviformica) fusca L. is a eurytopic (ubiquitous) species. These non-territorial, non-aggressive and typically submissive, so-called opportunistic ants are the widely known most frequent slave species of *F. sanguinea* (see, for instance, Hölldobler and Wilson 1990, Czechowski *et al.* 2002).

F. (Serviformica) cinerea Mayr is an oligotope of dry grasslands (also frequent in light pine forests). These aggressive, most probably territorial ants may yet also be enslaved by *F. sanguinea* (see Czechowski and Rotkiewicz 1997).

Larvae of the ant lion *Myrmeleon formicarius* L. (Neuropteroidea) live at very great densities in open sandy areas at that site (Fig. 1). Nuptial flights of ants of various species (Fig. 2) and raids of *F. sanguinea* provide them with excellent occasions for predation on ants.

A part of the data reported in this paper has been collected during accidental observations of encounters between ant lion larvae and workers of *F. sanguinea* made during the field research devoted to raiding activities of these ants, carried out in the Tvärminne dunes in the years 1998-2001.

In early July 2000, an additional experiment was also carried out in which the encounters between ant lion larvae and workers from a natural mixed colony of *F. sanguinea* and *F. fusca*, and from two monospecific colonies of *F. fusca* were provoked. During that experiment, four flat rectangular plastic containers (2822 cm) filled with sand and containing each 12 big larvae of the ant lion (*M. formicarius*) were placed near ant nests in a way which allowed the ants free access to them. Two containers were embedded in the sand close to a large *F. sanguinea* nest with *F. fusca* as a slave species (Fig. 3), and two remaining containers were placed close to each of two monospecific nests of *F. fusca* (Fig. 4). Both the natural course of events and the responses of the ants to a situation in which their nestmate was offered to an ant lion larva by the experimenter were observed. The ants used as victims in that experiment were captured by means of tweezers and then released directly into the mandibles of an ant lion larva. That experiment was continued during three successive days. Altogether, the course of events taking place during 24 cases of capture of a worker of *F. sanguinea* and during 10 cases of capture of a worker of *F. fusca* was observed.

We also report a detailed description of rescue behaviour of workers of yet another ant species, *F. cinerea* Mayr, induced in response to capture of a conspecific ant (most probably their nestmate) by a larva of the ant lion (*M. formicarius*). That event was observed
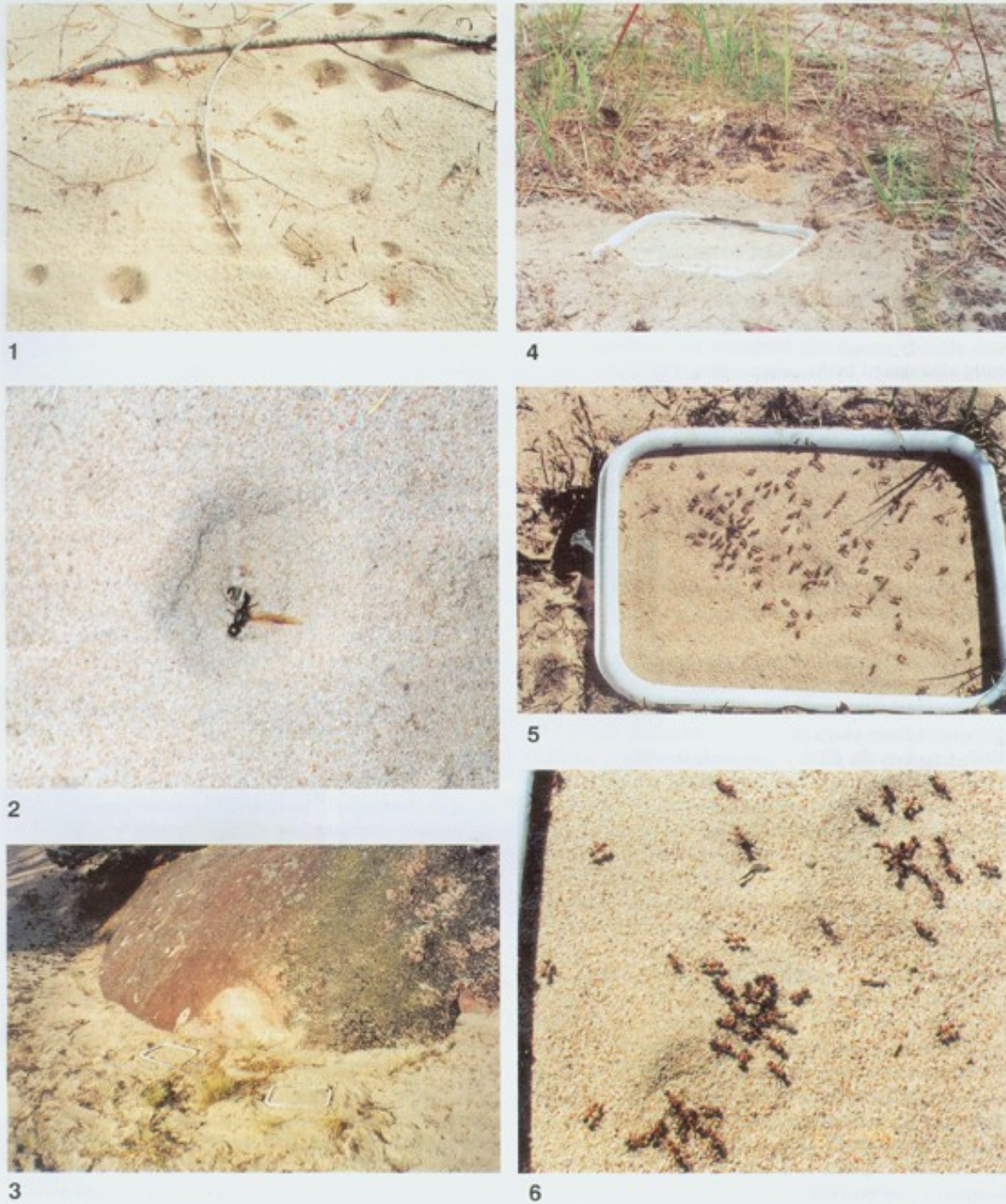
Figure 1–6. (1) Amassed pits of ant lion larvae, *M. formicarius*, on dunes at Tvärminne, Finland; (2) an alate queen of *Camponotus herculeanus* (L.) captured by an ant lion larva on dunes at Tvärminne; (3) two containers with ant lion larvae placed near a nest of the mixed colony of *F. sanguinea* and *F. fusca*; (4) a container with ant lion larvae placed near a nest of *F. fusca*; (5) situation in the container with ant lion larvae placed near the mixed *F. sanguinea + F. fusca* nest just after its insertion. One *F. fusca* worker can be seen (in the right bottom corner) in the middle of about one hundred *F. sanguinea* workers. In the left half of the container, ants are converging near the first victim of the ant lion; (6) three simultaneous rescue operations carried out by *F. sanguinea* workers. (Photos W. Czechowski).

on a coastal dune near Lubiatowo (the Baltic Coast, N Poland) on 2 June 2001, during an early afternoon, at sunny hot weather. At that site, the density of ant lion pits was relatively high. Scattered workers of *F. cinerea* could also be observed to forage on that dune.

The observation of capture of *F. cinerea* by an ant lion larva was carried out accidentally. The attention of the observer was attracted by a fountain of sand and concentrated activity of the ants at that spot. The event was recorded by means of a DVC camcorder supplied with an enlarging lens. The recording started at the moment when the victim seized by an ant lion larva was still visible above the sand surface together with several conspecifics moving around. It ended when the victim was already completely buried in the sand and apparently abandoned by its conspecifics. The whole recording session consisted of 127 seconds, with a 110 second break in the middle. The recorded material was analysed frame by frame by the aid of iMovie 2.1 application and a calculatory sheet.

RESULTS

Responses of workers of *F. sanguinea* to their nestmates attacked by ant lion larvae during raids

On the Tvärminne dunes, *F. sanguinea* raids mainly *F. cinerea* colonies which generally form vast polydomous systems there. *F. cinerea* are very efficient at defence of their nests (see Czechowski and Rotkiewicz 1997, Czechowski 1999, 2001) and, therefore, conflicts between these species are long-lasting and great numbers of attackers scatter over many square metres. It was frequently observed that blood-red ants participating in these raids fell prey to ant lion larvae which, under such circumstances, did not even bother to make pits, but attacked the ants directly from under the surface of the sand. Each capture of a blood-red ant induced a violent response of several to over a dozen nestmates present nearby. Similarly as in the case of the preliminary observation described in the introduction, this time, too, rescue behaviour shown by the ants involved both the attempts to pull the attacked ant away by tugging at its limbs, and furious brushing away of the sand in an apparent attempt to reach the ant lion. However, the ants never resulted to pull the ant lion larva on the surface of the sand.

Responses of workers of a mixed colony of *F. sanguinea* + *F. fusca* to their nestmates attacked by ant lion larvae placed experimentally close to their nest

*F. sanguinea* respond very fiercely to any activity near their nest. At the start of the experiment very numerous (over 100) aggressively disposed workers immediately ran into a freshly inserted container (Fig. 5). Within a few minutes, the ant lions present in the container began to catch these ants directly from under the sand, without digging any pits. Each capture of an ant by an ant lion released immediately a violent response of its nestmates. Each time several to over a dozen workers rushed to the victim and then showed typical rescue behaviour, involving both pulling at the limbs of the victim and furious digging around it. This behaviour continued until the victim had stopped to show any signs of life. Then, after few minutes, the ants usually ceased to show any further interest either in their nestmate, or in the ant lion. Altogether, 20 cases of such rescue behaviour were recorded during that initial part of the experiment. In one container four simultaneous rescue operations were even observed (Fig. 6).

The blood-red ants acting in the containers were accompanied by their slaves (in the proportion: a few slaves per a few score of *F. sanguinea* workers). The slaves behaved in the same way as did the blood-red ants; they were very excited, ran from victim to victim and joined the rescue operations. This initial excitement lasted for about an hour, until the hunting activity of the ant lions stopped.

When the observations were resumed after a few hours' break, there already were some pits in the containers. A *F. sanguinea* worker, captured at a relatively long distance from the containers (to avoid to alarm the ants present in the vicinity of the container) was placed, with great care, directly in the mandibles of the ant lion in one of the pits in the container I. At the moment when the ant lion seized that worker, the previously ant-free container was stormed by about 20 blood-red ants, running to rescue their nestmate. As a consequence, several seconds later another ant lion spontaneously caught a victim which had fallen into its pit. This event also provoked a fierce response of the ants and induced typical rescue behaviour, involving both pulling at the limbs of the victim and intense and rapid digging behaviour.

To compare the responses of the ants to captured workers of *F. sanguinea* and *F. fusca*, an enslaved worker of *F. fusca* was then offered to one of the ant lions from the container II, in which, at that moment, only over a dozen of relatively calm blood-red ant workers were present. That ant was captured and offered to the ant lion in exactly the same way as workers of *F. sanguinea*. However, its capture by the ant lion did not induce any change in the behaviour of the blood-red ants present in the container. Only one individual looked into the pit with the struggling victim and then indifferently went away.

The next two enslaved *F. fusca* individuals were offered to the ant lion larvae in the container I, in presence of about a dozen excited blood-red ant workers. The first victim did not elicit any interest in workers of *F. sanguinea*, although a large group of them was trying to rescue their conspecific close by (at 10 cm only). In
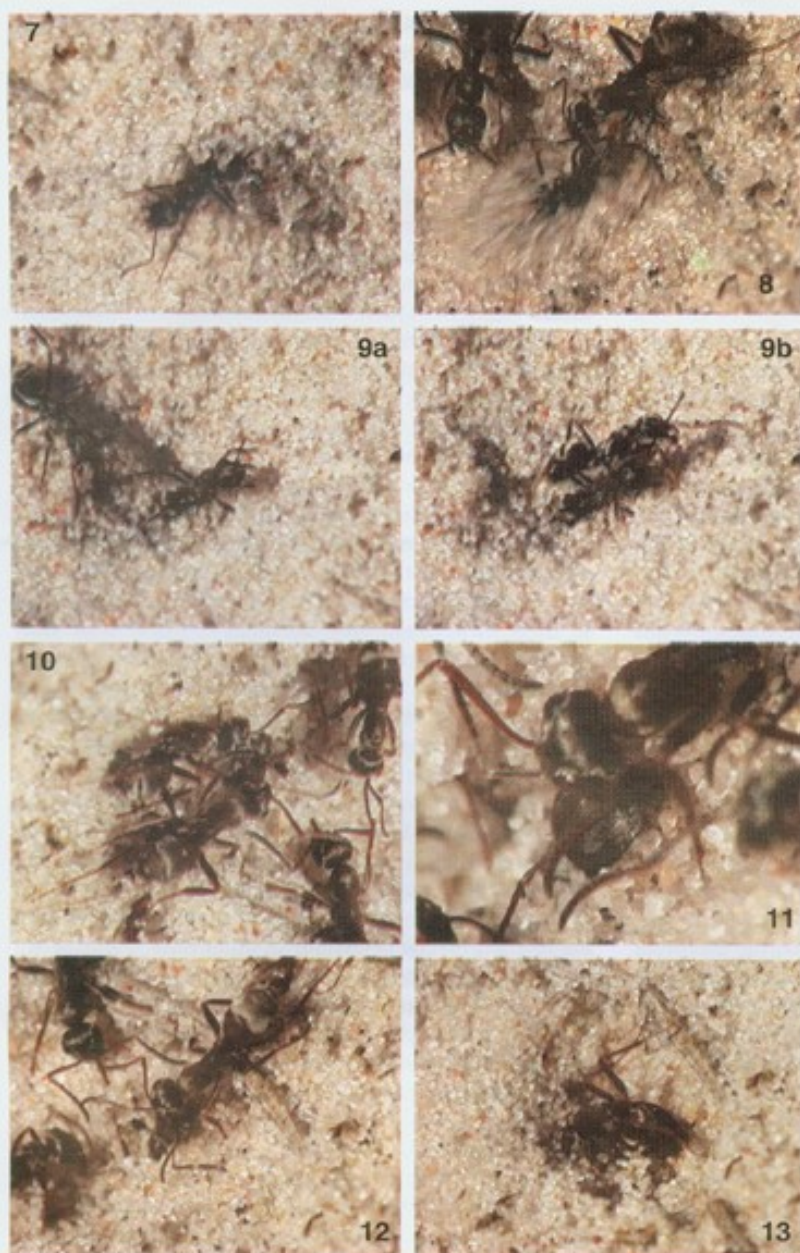
Figures 7–13. Frames of *F. cinerea* rescue operation selected from the video film recorded on the Baltic Coast, Poland (photo M. Kozlowski). (7) An ant lion larva catches a *F. cinerea* worker; (8) a sand fountain thrown up by an ant lion larva; (9a, b) *F. cinerea* workers approach a conspecific ant lion victim; (10) four *F. cinerea* workers in train of rescuing a conspecific ant lion victim; (11) rescue behaviour of *F. cinerea*: pulling of the attacked ant by an antenna; (12) two *F. cinerea* workers trying to pull away the ant lion victim (right side) and one more worker in train of digging (left side); (13) just before the end of the rescue operation, the last rescuer ant bends its gaster forward (possibly to spray the ant lion larva with the formic acid).

to the place where the ant lion had just moved. This worker, too, left the pit after a few seconds. In both these cases, the *F. sanguinea* workers seemed to be little aroused. A few minutes later, two ant lion larvae in the same container almost simultaneously caught blood-red ants. Several their conspecifics immediately rushed to each of the sore points, and one of the rescue teams was joined by a *F. fusca* worker.

On the following day, an enslaved worker of *F. fusca* was again offered to one of the ant lion larvae present in the container I. Two blood-red ants were present close by, but neither of them showed any response to that situation, and one even passed, unconcernedly, by the pit with the struggling victim.

Finally, yet another enslaved worker of *F. fusca* was offered to one of the ant lion larvae present in the container II. At that moment, no other ants were present in that container, but *F. sanguinea* were artificially disturbed by us at their nest and in this way over a dozen individuals were provoked into running into the container. However, on entering the container with the struggling victim, the blood-red ants calmed down and then turned back to their nest. This situation was altogether repeated three times.

Responses of workers of a monospecific colony of *F. fusca* to their nestmates attacked by ant lion larvae placed experimentally close to their nest

The tests with workers from monospecific colonies of *F. fusca* were much more difficult to carry out than the tests in which workers from a natural mixed colony of *F. sanguinea* and *F. fusca* were used as subjects. All the activities of the experimenter taking place close to

the second case, one worker of *F. sanguinea* entered the pit, for a few seconds was pulling lazily the antenna of the victim, and then left the pit. About a minute later, another worker of *F. sanguinea* entered that pit and, ignoring the victim, started to brush away the sand close

such a nest (including his attempts to capture an ant which could then be offered as a victim to an ant lion larva) had the same effect: *F. fusca* workers immediately retreated to their nest. Thus, solely in the case of three victims (taken from two monospecific colonies of *F*

fusca) the observations were carried out under conditions comparable to those employed before, during the tests in which we used as victims enslaved workers of *F. fusca* taken from a natural mixed colony of *F. sanguinea* and *F. fusca*. Only in these three cases the experimenter was able to capture the ant near its nest and then to offer it to an ant lion (in its pit in the container) without having alarmed other ants present close to the nest. In all three cases, desperate attempts of the victims to escape from the ant lion's mandibles were met with a total indifference of its nestmates present nearby.

Rescue behaviour of workers of *F. cinerea* shown in response to a conspecific worker attacked by an ant lion larva in the field

The victim was captured by the ant lion on the flat sand and the ant lion larva was not visible throughout the observation. The position of the body of the victim suggested that it was seized by the hind part of the gaster (Fig. 7) and then pulled down into the sand by means of repeated tugging movements. At times, the ant lion threw a small sand fountain (Fig. 8). Several conspecific ants started to approach the victim almost immediately after its capture. Approaching ants first stopped for a while with extended antennae and then rushed to the victim with opened mandibles, apparently searching for a good grip (Fig. 9a, b). At most four ants were recruited simultaneously to the victim (Fig. 10). Very soon, two ants working in concert seized the victim by its limbs and then persistently tried to pull it away (Fig. 11). One of these ants seized the base of the left antenna of the victim, the other ant seized the end of its left front tibia. Other ants in the view also approached the struggling victim and tried to dig close to it. However, the bouts of their digging behaviour were relatively short (maximum length of a digging bout: 7 seconds), and when they stopped digging, they left the victim (Fig. 12). The ant engaged in pulling the victim away by the antenna continued to display rescue behaviour during the longest time (altogether, 119 seconds). The worker pulling the front leg of the victim approached the victim later and was engaged in pulling it during a shorter time (65 seconds), all that time working in concert with the ant pulling at the antenna of the victim. During the next 14 seconds it continued to stay close to the victim and finally abandoned it. The ant engaged in pulling the victim by the antenna was the last among the rescuers to leave the victim. It left the victim only when it disappeared completely in the sand as a result of final strong tugs of the ant lion. During the final 7 seconds of its rescue action that ant was also observed to bend its gaster in the direction of the disappearing victim (or perhaps in the direction of the ant lion) (Fig. 13). However, it is impossible to tell whether that threatening posture was actually accompanied by the ejection of

venom. When that last ant finally left the victim, no further signs of interest of the ants either in the ant lion, or in its victim, could be anymore detected.

DISCUSSION

Our present data support our initial hypothesis that in a life-threatening situation workers of *F. sanguinea* emit some signals which effectively summon their nestmates to arrive at their rescue. Participation of enslaved individuals of *F. fusca* in these rescue operations suggests that these signals can also act in a cross-specific way. However, it is also possible that *F. fusca* joined these rescue operations in response to some signals emitted by their excited heterospecific nestmates already engaged in rescue behaviour, and not directly in response to danger signals emitted by the victims of the ant lions.

Very interestingly, workers of *F. fusca* show nestmate rescue behaviour in response to ants from other species, but they do not show that behaviour in response to their own conspecific nestmates. Workers of that species captured by ant lion larvae also fail to trigger rescue behaviour in their heterospecific nestmates, i.e., workers of *F. sanguinea* inhabiting natural mixed colonies of these two species. These data support our earlier hypothesis that workers of *F. fusca* captured by ant lion larvae do not emit danger signals able to elicit nestmate rescue behaviour either in conspecific, or in heterospecific (*F. sanguinea*) nestmates. It must be stressed that this does not imply that *F. fusca* do not emit any danger signals: however, these signals clearly fail to elicit rescue behaviour in other ants.

We also demonstrated that rescue behaviour closely similar to that shown by *F. sanguinea* is displayed also by *F. cinerea*, the second (after *F. fusca*) most important host of blood-red ants. However, in respect of bionomics that species is considerably different from *F. fusca* (see Czechowski and Rotkiewicz 1997, Czechowski 1999, Czechowski 2001).

Presence/absence of rescue behaviour (a fairly sophisticated form of co-operative behaviour) in the studied ant species is closely related to their biology and life strategies, and, in particular, to their positions in the interspecific competition hierarchy present within the ant community to which they belong. According to the theory of hierarchic structure of ant communities (see Vepsäläinen and Pisarski 1982, Pisarski and Vepsäläinen 1989) *F. sanguinea* and *F. cinerea*, both of them highly aggressive, territorial species, represent the 3rd (and the highest) level in the interspecific competition hierarchy (Czechowski 1999). Territoriality, which consists in guarding and defending the boundaries of foraging areas from alien (conspecific or heterospecific) colonies of other territorial ants, requires high level of co-operation of workers acting outside the nest, including efficient

systems of long-range recruitment to danger spots. *F. sanguinea* also makes well-organized dulotic raids against colonies of slave species (see Mori et al. 2000, 2001), and *F. cinerea*, as one of the latter, is known for its ability for well-organized defence (even in the foreground of the nest) against such attacks (Dobrzańska 1976, Dobrzańska and Dobrzański 1962, Czechowski 1975, 1977, 1999, 2001). Thus, both species are particularly well-adapted to combat, and nestmate recruitment towards endangered nestmates, clearly manifesting itself during territorial conflicts (Czechowski, unpubl.) is one of these adaptations. Moreover, workers of both species often undertake collective hunting and collective transport of large prey (Czechowski, unpubl.), and for these activities, too, efficient remote communication is indispensable.

In contrast to *F. sanguinea* and *F. cinerea*, *F. fusca* is a non-aggressive, non-territorial submissive species belonging to the 1st, lowest level in the interspecific competition hierarchy (see Savolainen 1989). These ants defend neither any territory boundaries, nor even their food sources. Their foraging strategy consists in incessant, very quick searching of their trophic area by single workers collecting tiny bits of food (Savolainen 1989). It even seems, in our opinion, that large aggregations of individuals gathering near larger prey items are not formed as a result of nestmate recruitment to food, but arise simply as a result of accidental finding of these prey items by successive individual foragers. Collective transport is unskilful and *F. fusca* often lose large prey items to the advantage of ants from species belonging to higher levels in the interspecific competition hierarchy, for instance, *Tetramorium caespitum* (L.), a species known to defend food sources, and, thus, belonging to the 2nd, intermediate level in the interspecific competition hierarchy (Czechowski, unpubl.). *F. fusca*, as a representative of the 1st level of the ant competitive hierarchy, defend only the nest (see Vepsäläinen and Pisarski 1982, Pisarski and Vepsäläinen 1989) and when they are attacked by their main enemies, *F. sanguinea* and *Polyergus rufescens* (Latr.), even their nest defence is as a rule very short and chaotic. Moreover, it is undertaken by just a few workers, without any signs of cooperation and/or mutual help (e.g. Dobrzańska 1976, Czechowski, unpubl.).

In view of that general absence of (at least distinct) helpfulness in intraspecific relations in *F. fusca* it is intriguing that enslaved workers of this species living in mixed colonies with *F. sanguinea* are, nevertheless, ready to show rescue behaviour in response to their heterospecific nestmates captured by ant lion larvae. This implies that, in spite of the fact that *F. fusca* workers fail to induce rescue behaviour in their nestmates, the overall behavioural repertoire of *F. fusca* includes still the behavioural pattern of nestmate rescue behaviour. This in turn strongly suggests that inability of *F. fusca* to elic-

it rescue behaviour in their nestmates is a derived evolutionary trait, and that the expression of nestmate rescue behaviour in enslaved workers of that species represents a form of atavism, a vestigial behavioural pattern retained from some earlier stage of the evolutionary history of that species.

Expression of nestmate rescue behaviour in enslaved *F. fusca* workers may be related simply to the fact that danger signals emitted by their host species, *F. sanguinea* (and/or signals emitted by *F. sanguinea* workers already engaged in rescue operations around ant lion victims), possess a sufficient behaviour-releasing capacity to attain the threshold necessary for the expression of that behaviour. Pheromone affinity (and communication affinity in general) between social parasites and their hosts, a prerequisite necessary for the existence of mixed ant colonies, seems now to be demonstrated without any doubt (see D'Ettore and Heinze 2001).

However, it cannot be excluded that the expression of nestmate rescue behaviour in *F. fusca* individuals from mixed colonies of *F. sanguinea* and *F. fusca* is related to some more general, non-specific modifications of the physiological state of these enslaved ants. These modifications, arising as a result of their rearing and subsequent life within a mixed colony, may then exert a modulatory action on the expression of various behaviour patterns. Behavioural repertoire of *F. fusca* workers contains other elements which are expressed only in enslaved individuals of that species living in mixed colonies together with their social parasites (*F. sanguinea*, *P. rufescens*), but which are not observed in normal monospecific colonies of *fusca*. One of these behavioural traits (important for our present discussion) is the level of extranidal aggressiveness, considerably enhanced in enslaved workers (Dobrzańska and Dobrzański 1960, Dobrzańska 1976). As a consequence, some slaves may even participate in raids and in robbing of pupae from alien nests (Czechowski, unpubl.).

Nestmate rescue behaviour described by us in the present study involved, on one hand, the attempts to rescue the victim of the ant lion (and/or the attempts to attack the ant lion) and, on the other hand, digging behaviour. Similar close interrelationship between alarm and digging behaviour was already described in several ant species. In particular, many authors reported that alarm and digging behaviour may be released by the same chemical compounds. As demonstrated by Wilson (1958), workers of *Pogonomyrmex badius* (Latr.) (subfamily Myrmicinae) respond to compounds present in the mandibular gland secretion of that species by alarm behaviour and, after some delay, also by digging behaviour. The same effects could also be observed as a result of exposure of the ants to a whole range of other relatively volatile chemical substances. Similarly, McGurk *et al.* (1966) showed that 4-methyl-3-heptanone present in the mandibular secretions of

Pogonomyrmex barbatus F. Smith acts both as an attractant and as a releaser of attack behaviour (involving biting and stinging). After a more prolonged exposure to that ketone, the ants also started to carry pebbles in their mandibles and (however, not frequently) to make digging movements with their legs. Interestingly, a closely similar interrelationship between alarm and digging behaviour was also reported in ants of other subfamilies (Dolichoderinae and Ponerinae). Thus, 2-heptanone present in anal glands of the dolichoderine ants, *Conomyrma pyramica* (Rog.), acts as a strong releaser of alarm, as a powerful attractant, and also as a strong releaser of digging behaviour (Blum and Warter 1966). Similarly, alarm secretions from the venom gland enhance digging activity in ponerine ants of some species of the genus *Leptogenys* Rog. which employ digging when hunting for animal prey (Maschwitz and Mühlenberg 1975).

According to Hangartner (1969), rescue behaviour shown by ants towards their nestmates trapped in sand or clay has been described already by Belt (1874) and Lafleur (1940). Stimuli eliciting and guiding the rescue digging behaviour were then investigated in numerous studies. The importance of chemical stimuli in the control of that behaviour, signalled already by Wilson (1958), Blum and Warter (1966), and Mc Gurk *et al.* (1966), was confirmed by Spangler (1968) who demonstrated that workers of *Pogonomyrmex occidentalis* (Cresson) respond by attraction and digging not only to whole buried workers, but also to parts of their bodies, and to larvae and pupae. These responses disappeared in workers deprived of their antennae. Hangartner (1969) showed that workers of *Solenopsis geminata* (F.) respond by rescue digging behaviour to low concentrations of CO_2 released both by living ants, and as the product of decomposition of their dead bodies.

Stimuli of other modalities may also play important role in triggering the nestmate rescue behaviour. Markl (1967, 1973) showed that in ants of the genus *Atta* F. rescue digging towards nestmates trapped in subterranean nest chambers is triggered by vibration signals produced by them by means of stridulation. Stridulation signals also enhances digging behaviour in the ants of the genus *Aphaenogaster* Mayr (= *Novomessor* Em.) but only in workers already engaged in digging activities, acting as a modulatory communication signal (Markl and Hölldobler 1978, Hölldobler and Wilson 1990).

The exact nature of danger signals emitted by workers investigated in our present study remains unknown. Failure of *F. fusca* workers struggling violently with the ant lion to elicit nestmate rescue behaviour strongly suggests that some highly specific chemical stimuli must play a crucial role in the initiation of rescue activities. However, although vibrations produced by a struggling ant are, evidently, not sufficient to trigger these activities, they may, nevertheless, play some role in the main-

tenance of rescue operations: the ant lion victims were, as a rule, left to their fate when their movements ceased. Stridulation signals are hardly possible to be responsible for triggering nestmate rescue behaviour, because stridulation is not found in formicine ants (Hölldobler and Wilson 1990).

As already mentioned, some of the ants joining the rescue operations may also respond to stimuli emitted by the other rescuers, and not directly to the stimuli emitted by the victim. This question remains open. However, in any case, the participation of *F. fusca* workers in the rescue of their heterospecific nestmates provides a striking example of the ability of ants to engage in cross-specific communication and co-operation. The phenomenon of cross-specific communication is already well documented in ants (as well as in other social insects) and it is not limited to everyday contacts between the heterospecific individuals of the same mixed colony resulted from social parasitism. The so called "propaganda" pheromones emitted by various dulotic species play a very important role in the suppression of the defense behaviour of the raided ants (Regnier and Wilson 1971, Hölldobler 1973, Hölldobler and Wilson 1990). Cross-specific signalling play an important role in ritualized communication between competing syntopic ants, for instance, of the genera *Polyrhachis* F. Smith, *Oecophylla* F. Smith and *Camponotus* Mayr (Mercier and Déjean 1996, Mercier *et al.* 1998). The ants may also engage in interspecific trophallactic exchanges, which may lead to the so called "trophallactic appeasement" of aggression of heterospecific ants (for instance, Bhatkar and Kloft 1977, Bhatkar 1983, Hölldobler and Wilson 1990), and in interspecific trail following and trail sharing (see e.g. Djean 1996, Gobin *et el.* 1998, Mercier *et al.* 1998).

Our present data provide a starting point for further studies devoted to fuller unravelling of mechanisms underlying the phenomena reported. It may be hoped that that research may throw further light on factors intervening in the course of the evolution of co-operative behaviour in social insects.

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