POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	57	2	341–352	2009

Regular research paper

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CORPSE CARRYING IN ANTS (HYMENOPTERA: FORMICIDAE): BEHAVIOURAL SIDE EFFECT OF AGGRESSIVE AROUSAL OR COMPETITIVE SIGNALLING?

ABSTRACT: Some literature reports show that ants use bodies of their dead nestmates and other insect remains in conflict situations. The paper describes such phenomenon in a *Formica rufa* L. colony brought into conflict with a *F. cinerea* Mayr colony when the former tried to extend its own territory at the expense of the latter. A territorially stable *F. rufa* colony, neighbouring the same *F. cinerea* colony, served as control. Workers of the expansive *F. rufa* colony were repeatedly observed to carry numerous ant corpses, empty pupal cocoons and insect leftovers from their nest to the place of confrontation with *F. cinerea*, on a much bigger scale than workers of the stable *F. rufa* colony. Corpse-carrying intensity was not correlated with the general activity level of foragers which suggests that corpse carriers could be a separate task group. Workers of a small colony of *F. cinerea* were also observed to surround their nest entrance with corpses of their nestmates and prey remains, taken out from inside the nest, in response to intensified traffic of workers of *F. rufa* in the vicinity of their nest. These results are discussed in the context of a possible interrelation between ant aggressive behaviour and transport behaviour. Two hypotheses are proposed to explain the observed phenomenon: (1) explaining it as a by-product of the aggressive arousal of workers, and (2) ascribing to it a possible signalling function in conflict situations.

KEY WORDS: ants, *Formica rufa*, *Formica cinerea*, territoriality, interspecific competition, aggression, transport, communication, ant cemeteries

1. INTRODUCTION

In territorial ants of the subgenera *Formica* s. str. and *Coptoformica* Müll., dead individuals and other insect remnants are often taken out by the workers to the border of the territory (Dlusskij 1965, see also Lubicz Niezabitowski 1933). A similar situation is sometimes also encountered in non-territorial *Lasius niger* (L.), where one can see distinct linear 'cemeteries' a few metres in length, consisting of corpses and empty cocoons, partly surrounding the nest at a distance determined by the home range of the workers (Czechowski 1976). The submissive *Myrmica schencki* Viereck. nesting within territories of the dominant *Formica polyctena* Först. often surround their nest holes with piles of dead ant bodies placed directly outside the chimney-like nest entrances (Czechowski 2008). Similar deposits of insect remnants around the nest entrance were also found in *Formica rufibarbis* F. (Godzińska 1986).

To date there is no evidence pointing to any possible signalling role of such waste accumulations in relations amongst ants.

However, some observations have shown that ants may use corpses of their nestmates, empty pupal cocoons and insect leftovers in conflict situations, both inter- and intraspecific, of socially parasitic or competitive origin. Workers of *Formica sanguinea* Latr. were observed to carry out dead individuals from their own nest in the initial phase of slave raids and to deposit them in front of the target nests of *Formica cinerea* Mayr (Czechowski 1975, 1977) and (experimentally colonised) *F. polyctena*. (Czechowski 1989). *Lasius niger* showed the same behaviour when attacking *Myrmica rubra* (L.) to take over its nests (Czechowski 1985). During a break in several days' intraspecific combat, workers of two hostile *Formica exsecta* Nyl. colonies carried dead ants or empty cocoons from their nests and left them along a temporary 'demarcation line' (Czechowski 1990).

An especially spectacular behaviour of this kind was observed during the recent studies on the foraging strategies of *Formica cinerea* and its competition with other ant species (see Markó and Czechowski 2004, 2009, Czechowski and Markó 2005), including *Formica rufa* L. In boreal and temperate coniferous forests, *F. rufa* and other wood ants of the *F. rufa*-group, typically territorial and highly aggressive species, are unquestioned top dominants in multispecies ant assemblages, in terms of interspecific competition hierarchy (Savolainen and Vepsäläinen 1988, Pisarski and Vepsäläinen 1989). Their role in structuring entire assemblages is well-known, as are their relations with particular subordinate ant species (Savolainen and Vepsäläinen 1988, 1989, Savolainen *et al.* 1989, Punttila *et al.* 1991, 1996, Czechowski 2000, Vepsäläinen *et al.* 2000, Czechowski and Vepsäläinen 2001, Czechowski and Markó 2006). *F. cinerea* may play a similar role in sun-exposed sandy habitats (like coastal and inland dunes) and light thin pine forests as an aggressive and at least potentially territorial species (see Zhigulskaya 1971a, b, Czechowski 1999, Markó and Czechowski 2004, 2009, Czechowski and Markó 2005).

2. STUDY AREA, MATERIAL AND METHODS

2.1. General information

The studies were carried out in a complex of sand dunes overgrowing with pine forest near the village of Tvärminne on Hanko Peninsula in southern Finland. The dominants of the local ant communities were *F. cinerea* (in relatively open areas) and *F. rufa* L. (in more tree-covered areas). Within the dune complex, in places where expanding forest patches intermingle with open sandy areas, the habitat, in the course of the succession, starts to be appropriate for *F. rufa* and at the same time it is still appropriate for *F. cinerea*. Consequently, these two species occur side by side and compete with each other (see Markó and Czechowski 2004, 2009). The observations reported here were carried out in such an area (see Figs 1 and 6 in Czechowski and Markó 2005) from 22 July to 6 August 2005.

To induce direct confrontations between the competitors transects of baits connecting some of the *F. rufa* and *F. cinerea* colonies were set. Flat plastic caps (Ø 2.5 cm) filled with water solution of orange syrup, placed at 1 m intervals, were used as baits. For an arrangement of the bait transects see Fig. 1

Table 1. Dynamics of traffic of various categories of workers of *F. rufa* along particular transects (see Fig. 1): medians (and lower and upper quartiles) of the numbers of workers crossing the frame (Fig. 2) while going from their nests within five minutes. The results of statistical analyses of these data are given in the text.

Transects (No. of individuals)	FR-3→FC-1 (n = 36)	FR-3→FC-X (n = 30)	FR-4→FC-1 (n = 18)	FR-4 regular route (n = 18)
Non-carriers	17 (13-21)	27.5 (12-41.5)	14 (14-15)	41 (36-45)
Corpse and cocoon carriers	1 (0-3)	2 (1-3)	0 (0-1)	0 (0-0)
Total	18 (15-22)	28.5 (14-43.5)	14 (14-16.5)	41 (36-45)

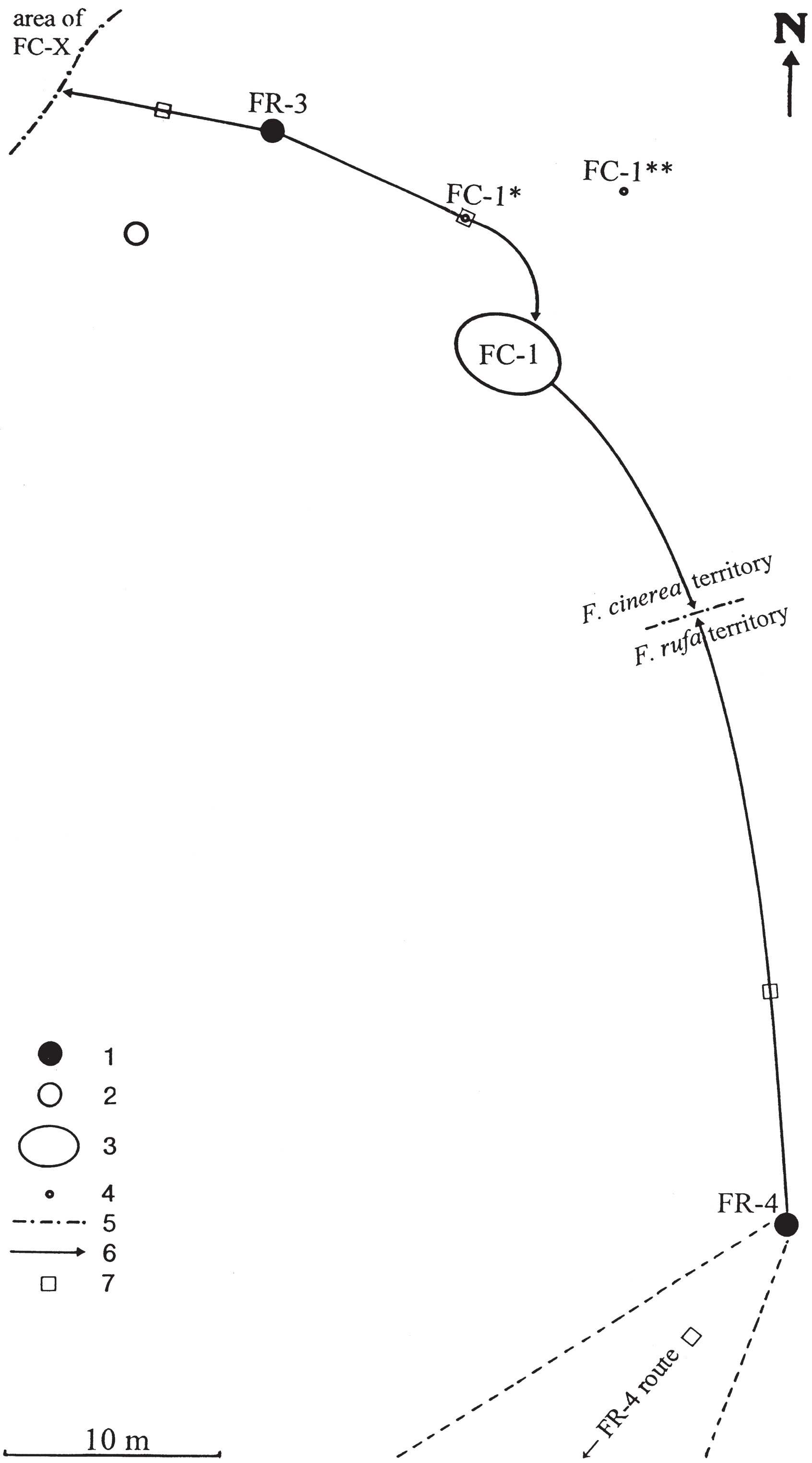

Fig. 1. Map of the studied *F. cinerea* (FC) and *F. rufa* (FR) colonies and the situation of bait transects in June 2005 (for details concerning colony symbols see the text); 1 – nest of *F. rufa*, 2 – abandoned nest of *F. rufa* FR-3, 3 – nest area of polydomous colony of *F. cinerea,* 4 – single nest of *F. cinerea*, 5 – border between the territories of *F. rufa* and *F. cinerea*, 6 – bait transect, 7 – position of biocoenometric frame.

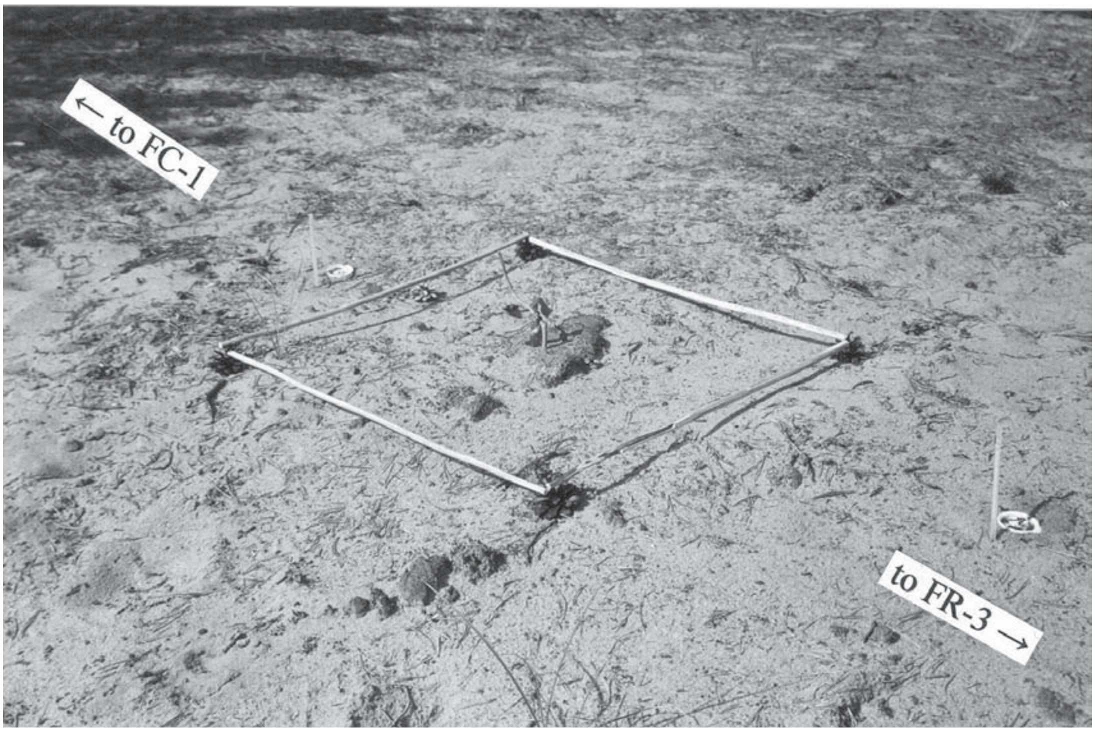

Fig. 2. Biocoenometric frame (0.5 × 0.5 m) placed between two baits (marked with white plastic sticks), comprising the nest of *F. cinerea* FC-1* (under a patch of moss; marked with a twig with a ribbon). (Photo by W. Czechowski, taken in late July 2005).

and Results. To estimate the intensity of ant traffic along the transects, biocoenometric frames of 0.25 m^2 (0.5 × 0.5 m) were placed within the ant routes – in the same place between two baits (Fig. 2) – and workers entering them during a chosen time unit (5 minutes) were counted, including those carrying corpses and other insect remains, as well as empty cocoons. The same, as a control, was done within a regular ant route of the colony FR-4 (see Results). Between 18 and 36 repetitions of that procedure were made in the case of each of the transects (see Table 1). For each transect (route), all measurements were carried out on a single day and were evenly arranged into three series: morning, afternoon and evening. Measurements with biocoenometric frames lasted four days following (one day per one transect) at the end of July and the beginning of August, during stable fine sunny weather.

Non-parametric tests were used for statistical analysis of these data as even the $\log_{10}$-transformed datasets failed to meet the requirements of the Kolmogorov-Smirnov test of normality. Kruskal-Wallis ANOVA and Mann-Whitney U-tests were applied to compare the datasets. Fisher Exact Probability Test and Spearman rank-correlation tests were also used. We used table-wide sequential Bonferroni-correction (Rice 1989) for revealing the exact significance level when performing multiple analyses of related datasets (*e.g.* multiple Spearman rank-correlations, pairwise Mann-Whitney U-tests carried out after a Kruskal-Wallis analysis).

2.2. Ant colonies involved and the situation preceding the main observations

In 2002, when the studies on competition between *F. cinerea* and *F. rufa* on Tvärminne dunes were started, the observed complex of *F. cinerea* colonies (consisting of a few nest systems) was surrounded by a ring of *F. rufa* nests (FR-1, FR-2, FR-3, FR-4). In 2004, it was additionally noticed that the territories of the *F. rufa* colonies hardly touched the range of *F. cinerea* workers, so that the ants of these two species did not directly contact each other, except over a short (2–3 m) stretch of a well-visible border, guarded on both sides, between the territory of *F. rufa* colony FR-4 and the range (in this case one should say "territory") of a polydomous *F. cinerea* colony FC-1, a member of the above mentioned *F. cinerea* complex (see Figs 2 and 4–6 in Czechowski and Markó 2005). The border was renewed in the following years (up until 2008, when the observations were completed) through intermittent hostile encounters of the two species in the springtime.

This relatively stable situation lasted till the spring of 2005, when the colony FR-3 of *F. rufa* abandoned its old nest and built a new one at a distance of *ca* 8 m from the former nest site (dimensions of the new mound: Ø 90 cm, h 20 cm). That nest relocation destroyed the established territorial arrangement, as *F. rufa* started to explore the new terrain intensely, encroaching on the area of *F. cinerea*'s complex. As a result, some of the colonies within this complex found themselves within the range of *F. rufa* workers. In particular, this happened to two small monodomous colonies FC-1* and FC-1**, and to a marginal part of the nest area of a large polydomous colony FC-1 (*ca* 5.5 m in diameter; see Fig. 2 in Czechowski and Markó 2005), situated, respectively, 9, 16 and 13 m away from the new nest of FR-3 (Fig. 1; compare Fig. 6 in Czechowski and Markó 2005). This new situation made possible to investigate the differences in the relationship between *F. cinerea* and a territorially stable colony of *F. rufa* (FR-4) *vs* a colony of that species (FR-3) just expanding its territory by conquering a new area.

3. RESULTS

The baiting experiment (27–29 July) triggered only a very weakly expressed border conflict between the stable *F. rufa* colony (FR-4) and *F. cinerea* (FC-I). Although though heterospecific workers, more abundant than usually, encountered one another at the border, only sporadic short-lived skirmishes were seen, and foragers of each species exploited only the baits on their own side of the border (Fig. 1). The situation was totally different in the case of the expansive colony of *F. rufa* (FR-3). Workers from that colony occupied all the baits of the two transects and tried both to enter the nest area of FC-1 and cross the border line of FC-X (Fig. 1). After the initial success, they were held off by workers of *F. cinerea*, which were only then mobilised into action. Several ants were killed on both sides on each of these two fronts.

In the course of these conflicts, amazingly many *F. rufa* workers going from FR-3 along the bait transects (15 and 10 m long respectively) towards both FC-1 and FC-X areas carried corpses (or fragments of corpses) of their nestmates, empty pupal cocoons (25% of all registered loads) or, occasionally, remnants of various other insects. Such behaviour was also observed, although on a much smaller scale, along the transect (*ca* 40 m long) between the nests FR-4 and FC-1. To describe this phenomenon quantitatively, the dynamics of the traffic of *F. rufa* individuals going towards their target along the transects were determined using a biocoenometric frame (see chapter 2.1). The width of *F. rufa* routes along all these transects was similar and did not exceed 1 m. As a control, the same procedure was repeated within the main (and, in practice, the sole) regular route of the colony FR-4 leading from the nest, across an open sandy area, to a dense forest (*ca* 14 m away) where stretched out the main part of the territory of that colony. The route, fanned out from the nest, was about six metres (!) wide in that place; the frame was placed within the main current of the ant traffic.

On the average, every 16th and 15th *F. rufa* worker which crossed the frame when going from FR-3 nest towards the sites of conflict with *F. cinerea* (FC-1 and FC-X respectively), carried a corpse of a conspecific ant, an empty cocoon, or other insect remnant (counted without making distinction between various categories of loads). The ratio of numbers of non-carriers and carriers for these two routes was almost identical (751:50 and 808:56; Fisher Exact Probability Test: NS). In contrast, only six out of 274 *F. rufa* workers from FR-4 going to the border with *F. cinerea*, and only four out of 718 workers observed on the regular route of the same colony were seen to carry a corpse of a conspecific ant, undoubtedly carrying it to the usual dumping ground. No case of transport of a cocoon or of another insect remnant was observed (Table 1).

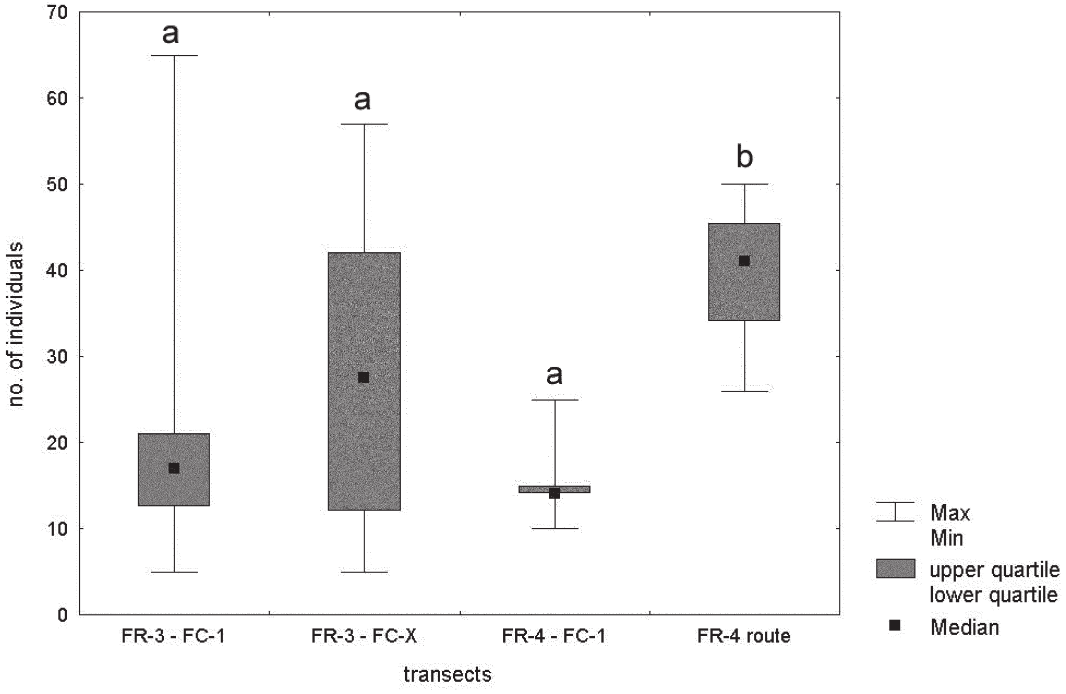

Fig. 3. Distribution of the numbers of the unloaded individuals entering the frame during five minutes (medians, quartiles, minimum and maximum values) among the four transects (see Fig. 1); n = 36, 30, 18, 18 respectively. Significantly differing groups: a and b (pairwise comparisons by means of Mann-Whitney U-test, $z \leq -2.622$, $P \leq 0.009$, Bonferroni correction applied).

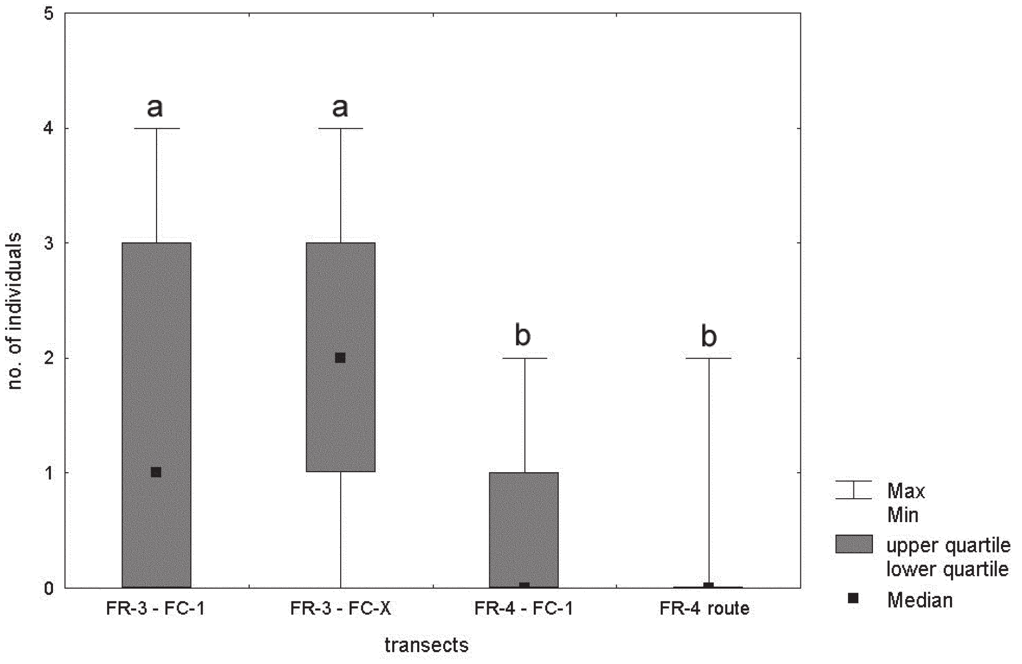

Fig. 4. Distribution of the numbers of the loaded individuals entering the frame during five minutes (medians, quartiles, minimum and maximum values) among the four transects (see Fig. 1); n = 36, 30, 18, 18 respectively. Significantly differing groups: a and b (pairwise comparisons by means of Mann-Whitney U-test, $z \leq -3.013$, $P \leq 0.003$, Bonferroni correction applied).

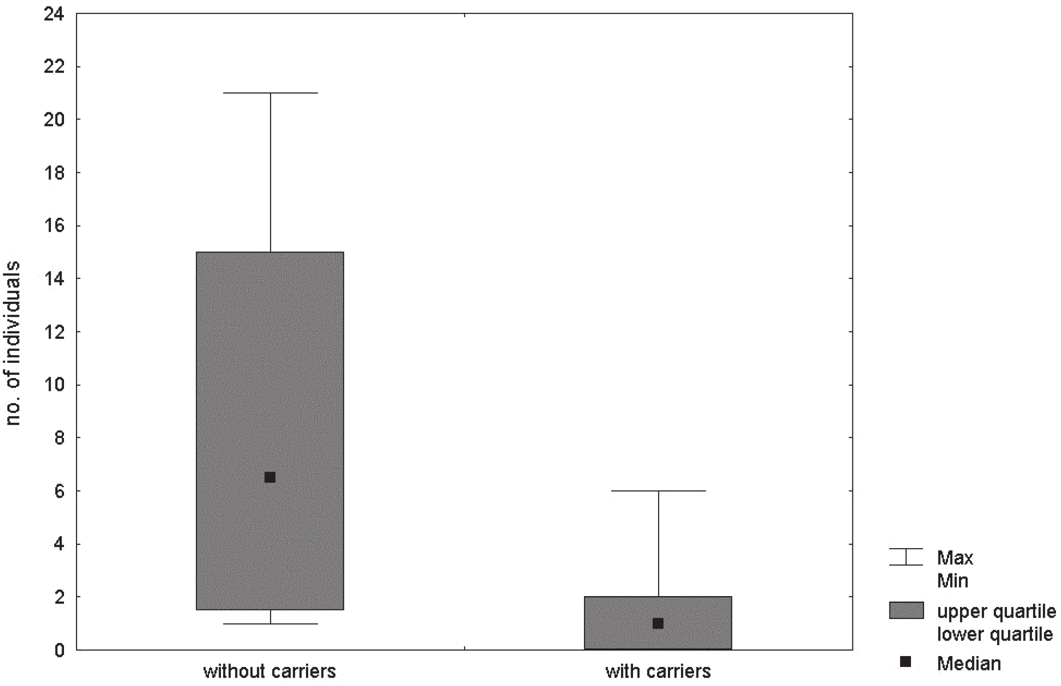

Fig. 5. Number of *F. cinerea* individuals leaving the FC-1* (see Fig. 1) colony during five minutes (median, quartiles, minimum and maximum values) in the absence (n = 12) and in the presence (n = 24) of carrier *F. rufa* ants.

Sometimes *F. rufa* workers were seen coming back with a corpse along the transect to their own nest, but that happened very rarely. Almost all such loads were left by them in the conflict regions. Ants would mostly put them directly before the front line. Some *F. rufa* workers, however, dodged between the defenders, trying to carry their loads deep into the hostile area. The 'record holder' in this hazardous venture, after crossing the border line between the territories of FR-3 and FC-X, went five metres down the sandy slope in zigzags, found the foreign nest, circled around it for a few minutes avoiding the attacking *F. cinerea*, put the corpse right at the nest entrance, and hurried along a straight line back into its own territory.

Corpse and cocoon carrying activity was apparently independent of the intensity of ants' foraging activity. A significant correlation between the number of carriers *vs* non-carriers was found only in the case of FR-4→FC-1 transect (Spearman r = 0.567, *P* = 0.014).

On the other hand, the number of non-carriers differed significantly among the four transects (Kruskal-Wallis test, $\chi^2 = 31.556$, $P < 0.001$, df = 3) (Fig. 3). Pairwise Mann-Whitney comparisons revealed that the number of such foragers was significantly higher on the route of FR-4 than on the other transects (in all three cases: Mann-Whitney z ≤-2.622, *P* ≤0.009, Bonferroni correction applied) (Fig. 3).

The number of corpse-carriers also differed significantly between the four transects (Kruskal-Wallis test, $\chi^2 = 27.08$, $P < 0.001$, df = 3) (Fig. 4). However, the pairwise Mann-Whitney comparisons revealed a different relationship than in the case of ants not engaged in corpse carrying. The number of carriers did not differ significantly between FR-3→FC-1 and FR-3→FC-X transects, but in both these cases it was higher than the number of carriers coming from FR-4 colony (transect FR-4 →FC-1 and the route of FR-4) (Fig. 4) (in all four cases: Mann-Whitney U-test, z ≤-3.013 *P* ≤0.003, Bonferroni correction applied).

In the transect from FR-3 to FC-1 the frame included the nest FC-1* (located in its middle) and the *F. rufa* route running across this nest of *F. cinerea* (Fig. 1). The frame was placed on that specific spot to observe simultaneously the activity of this small *F. cinerea* colony and the attitude of its members towards *F. rufa* workers (and *vice versa*). *F. cinerea* individuals leaving the nest as well as those coming back (*i.e.* entering the frame in both cases) were recorded. Median value of the number of workers leaving the nest/coming back = 2 (lower quartile = 1, upper quartile = 4 in both cases); median value of the total number of workers entering the frame (from the nest and from outside) = 3 (lower quartile = 2, upper quartile = 8), n = 36. For the dynamics of the *F. rufa* traffic recorded at the same time see Table 1.

FC-1* was a very small colony composed of a few small workers (typical of young colonies), much smaller that those of the colony FC-1. *F. rufa* workers going from the nest FR-3 (and back) along the bait transect to the nest area of FC-1 simply trampled on the nest FC-1* (Fig. 2). They paid no attention to the local *F. cinerea* individuals. Moreover, *F. cinerea* from FC-1* exploited the nearest baits simultaneously with *F. rufa*. However, both in the vicinity of their own nest and on the baits, the *F. cinerea* workers behaved towards *F. rufa* in a way resembling that of *F. fusca* L. – a typically opportunistic submissive species (see *e.g.* Savolainen 1990, 1991). The only active response of *F. cinerea* workers from FC-1* to intensified *F. rufa* traffic in the immediate vicinity of their nest consisted in taking their own nestmate corpses and insect remains out of their nest and putting them around the nest entrance.

The possible measurable effect of *F. rufa* activity on behaviour of workers of this small *F. cinerea* colony was analysed. Pairwise Spearman rank-correlation tests were applied to find the possible correlation between the number of *F. cinerea* individuals going out from the FC-1* colony and coming back to it, and the number of *F. rufa* corpse-carriers. Interestingly, no significant correlations were discovered between the number of corpse-carriers and the number of unloaded *F. rufa* individuals, but a significant negative correlation was detected between the intensity of corpse-carrying activity in *F. rufa* and the number of *F. cinerea* individuals leaving the FC-1* colony (Spearman r = -0.526, *P* = 0.001, n = 36, Bonferroni correction applied). A more robust analysis confirmed the latter finding: more *F. cinerea* individuals left the nest in the absence of corpse-carrying activity by *F. rufa* (Mann-Whitney U-test: z =-2.94, *P* = 0.003, $n_{without} = 12$, $n_{with} = 24$) (Fig. 5).

4. DISCUSSION

The fact that the level of corpse-carrying activity in *F. rufa* was not correlated with the general activity level of foragers suggests that corpse-carriers could be a separate task group, like guards well known in many ant species (*e.g.* Owen 1980, Déjean 1985, Champalbert 1986, Déjean *et al.* 1989, Aarab *et al.* 1990, Champalbert and Lachaud 1990, Déjean and Lachaud 1991, 1992, Jaisson *et al.* 1992), including those of the *F. rufa* group (*e.g.* Rosengren and Sundström 1987, Dorosheva and Reznikova 2006). If it were so, then their activity might have been triggered and influenced by other factors than those controlling the activity of the common foragers. Such guards might participate in the foraging process in general, but their presence might become more emphasised in situations with a high probability of conflict. Nevertheless, other factors triggering their activity, like the presence of new, unexplored areas (as in the case of FR-3 colony), also cannot be excluded.

Using corpses in conflict situations was observed not only in *F. rufa* during their offensive action against *F. cinerea*, but also in *F. cinerea* (FC-1*) during their defensive activity against *F. rufa*. If the concept of the guard role of the corpse carriers is right, the *F. cinerea* individuals, which took corpses out of their endangered nest and put them around the nest entrance could be described as 'defensive' guards, as opposed to 'offensive' guards of *F. rufa*, which transported the corpses from their nest to the front line of the ongoing conflict or even beyond it.

The existence of such behavioural subgroups among foragers, which could differ either in respect to their response thresholds, or in respect to types of activity employed during the foraging process, could play a decisive role in adapting the entire colony to changing conditions encountered during foraging (Sundström 1993, de Biseau and Pasteels 2000, Portha *et al.* 2004).

However, it must be stressed that the question of the existence of such specialised 'corpse-carrying guards' and of the possible signalling role of the corpse-carrying activity shown by the ants in the context of interspecific conflicts remains still open, as that phenomenon may also be explained in other, so far equally hypothetical ways. In particular, it should be remembered that in ants behavioural patterns underlying aggressive behaviour (including predatory behaviour) and transport behaviour are closely interrelated. For instance, workers of *Tetramorium caespitum* Mayr employ the same basic behaviour pattern when seizing prey and objects serving as building material (Dobrzański and Dobrzańska 1975). In young inexperienced workers of *F. rufa* and *F. exsecta* the transport of sticks serving as building material is a rule preceded by a "struggling" phase closely resembling both fighting behaviour and/or prey capture behaviour (Dobrzański 1971). It is also commonly agreed that transport and retrieval of seeds displayed by foragers of harvesting ants is most probably evolutionarily derived from their predatory behaviour, as both these types of behaviour involve a closely similar behavioural sequence (Horwitz and Beattie 1980, Déjean and Lachaud 1994, Godzińska 2004). The most extensive direct evidence that ant aggressive behaviour and transport behaviour are very narrowly interlinked was provided by Mabelis (1979) for *F. polyctena.* He showed that in these ants the transport of a congener worker (both nestmate and non-nestmate) is always preceded by the so called "aggressive phase" during which the transported ant is biting and/or pulling the future transport. Workers that specialise in congener transport also show higher readiness to engage in aggressive behaviour than their remaining nestmates, and they specialise in predation and/or scavenging rather than in foraging for carbohydrate food.

It must also be remembered that the ants relatively frequently engage in very unselective transport behaviour directed to various apparently useless objects such as small stones, inedible plant fragments, empty snail shells, bits of metal or plastic, and parts of arthropod corpses. Such behaviour was particularly frequently reported in harvesting ants of the genera *Messor* For., *Pogonomyrmex* Mayr and *Pheidole* Westw. (Tevis 1958, Jorgensen and Porter 1982, Hahn and Maschwitz 1985, Delalande and Lenoir 1987, Detrain 1990, Lopez *et al.* 1992, Godzińska 2004), and in the ants of the genus *Formica* L. (wood ants and *F. sanguinea*) (Marikovsky 1965, Chauvin 1968, 1969, Godzińska 1986, Rosengren and Sundström 1987).

Among numerous proximate and ultimate causal factors invoked by various authors to account for such unselective transport, of most interest are for us explanations which link the readiness for that behaviour with the state of arousal (excitement) and/or the so called high 'tempo'. The term 'tempo' was coined by Oster and Wilson (1978) to denote a whole complex of interlinked behavioural traits. Low-tempo workers were described by them as moving slowly and with seeming deliberation, examining objects carefully, and communicating with nestmates unexcitedly, while high-tempo workers were dashing about, skittish and excitable, and often mutually cancelling one another's actions (Oster and Wilson 1978, Hölldobler and Wilson 1990). The influence of tempo on readiness to transport various apparently useless objects was described in the *Formica* species already by Marikovsky (1965) who reported that such behaviour is most strongly expressed in large mature colonies in which ants have "all signs of surplus and unused energy". Delalande and Lenoir (1987) came to a similar conclusion in a choice experiment in which workers of the harvesting ant *Messor structor* (Latr.) could retrieve either whole seeds of ryegrass or their empty shells: the selectivity of the tested ants was negatively correlated with the intensity of the traffic at a given seed distributor. In the light of these data, it cannot be excluded that increased readiness of ants to transport corpses displayed by them in the context of conflict situations might have resulted from decreased selectivity of their transport behaviour arising as a result of arousal and/or increased tempo induced by behavioural context of defence and/or aggressive competition.

It is also possible that corpse-carrying behaviour observed in ants during conflict situations may represent an example of the behavioural phenomenon known as displacement activity, the notion applied to behaviour patterns seemingly irrelevant to the context in which they are observed. Displacement activities are known to appear commonly in various kinds of conflict situations (*e.g.* Slater 1999).

However, it should be stressed that all such hypothetical explanations pointing at the possible proximate causal factors of corpse-carrying behaviour do not exclude the possibility that corpse carrying may have some signalling role as well. Moreover, as well known, communication may involve two types of direct channels: signals (stimuli shaped by natural selection to carry information) and cues (stimuli containing information, but without having been shaped by natural selection to carry it, and conveying it only incidentally) (Lloyd 1983, Seeley 1989). In social insects, transfer of information through cues plays a very important role, often discussed in terms of the so called indirect social interactions (Michener 1974), or the information flow *via* shared environment (Seeley 1989).

The questions of proximate causation and possible signalling function of corpse-carrying behaviour shown by some ants in context of various inter- and intraspecific conflicts remain thus open for future investigations. Only further more detailed studies of that behaviour may resolve these questions in an unequivocal way.

Finally it is worth noting that, in the light of the presented findings and all our current knowledge on wood ants/*F. cinerea* relations (see Markó and Czechowski 2004, 2009), as well as in the general context of ants' territoriality, our observations of the mutual attitude of *F. rufa* and *F. cinerea* colony FC-1*, and especially of submissive, opportunistic conduct of the latter, provide further interesting information on that topic. This observation does not only support particularly well the hypothesis proposing that ant territorial behaviour undergoes important modifications as a function of colony age (size), but it also suggests that the colonies of the species occupying the medium level in ants' competition hierarchies, *i.e.* 'encounterness' (see Savolainen and Vepsäläinen 1989), do not reach that level from the very beginning of their existence as separate social units, but might need some time to attain it.

ACKNOWLEDGMENTS: The field observations were made during W.Cz.'s stay at the Tvärminne Zoological Station, University of Helsinki, within the programme of scientific co-operation between the Polish Academy of Sciences and the Academy of Finland. B.M.'s work during the preparation of the manuscript was supported by grant no. 31/1342 C.N.C.S.I.S. (2006–2008) and ID-552 PNII (2007–2009), and by PL-TAF-3066 Synthesys EU FP 6 research grant. E.J.G.'s work during the preparation of the manuscript was supported by the Statutable Grant 407 of the Nencki Institute of Experimental Biology of the Polish Academy of Sciences in Warsaw. The authors thank an unknown reviewer, whose accurate suggestions helped to improve the original version of the manuscript.

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Received after revising October 2008