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The effect of past and present group size on responses to prey in the ant *Formica polyctena* Först

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Abstract. We investigated the responses to insect prey (dead houseflies) in 24 "derivative groups" of workers of the ant *Formica polyctena* created by taking sets of 25 workers out of nine larger "initial groups" kept in laboratory without queens and brood during the preceding five months. In the derivative groups the ants ceased to retrieve flies to their nests after a period ranging from few days to several weeks. The duration of that period did not depend on the present size of the derivative group (decreasing as a result of worker mortality), but was positively correlated with the estimated size of the initial group of the tested ants. The readiness to display venom spraying was higher in smaller derivative groups. These data demonstrate that responses of *F. polyctena* to insect prey are strongly influenced both by the present and the past size of their group.

Key words: *Formica polyctena*, Formicidae, prey-predator interactions, scavenging behaviour, expression of behaviour, group size

INTRODUCTION

The ant species *Formica polyctena* Först. belongs to the wood ant group *F. rufa* (subfamily Formicinae). Mature colonies of wood ants retrieve to their nests large quantities of insect prey. As a result, in many countries these ants are used successfully to control forest pests (for recent reviews see Hölldobler and Wilson 1990, Way and Khoo 1992).

Ants may obtain proteinic food either by hunting for live prey (predatory behaviour) or by collecting dead prey (scavenging behaviour). A hunting ant must, in sequence, (1) locate a prey item, (2) subdue the prey, and (3) retrieve it to the nest. Each component of that sequence is also a sequence of events and may be decomposed into further subcomponents (Ayre 1968, Büttner 1973, 1974c, Herbers 1981).

Sequences of behavioural acts shown by formicine ants in response to live prey (hunting behaviour) and in response to dead prey (scavenging behaviour) were investigated, among others, by Ayre (1968), Büttner (1973, 1974c), Dejean (1988), Dejean et al. (1994) and Lenoir and Dejean (1994). That research revealed, among others, that behavioural sequences shown by these ants in response to live and dead prey are closely similar, with the only major exception: spraying the prey with the venom, the so called venom spraying, is displayed only exceptionally in response to dead or inert prey. Venom spraying appears particularly frequently in response to large and/or potentially dangerous prey, as it helps the hunting ant to subdue such prey without a direct contact (Dejean 1988, Dejean et al. 1994). Movements of the prey and/or its escape may also trigger venom spraying (Büttner 1973, Dejean 1988, Dejean et al. 1994).

Venom spraying helps the formicine ants to subdue prey not only as a result of a direct toxic action of the venom (Otto 1960, Cavill and Robertson 1965). Compounds released during venom spraying also play an important role in the chemical communication among the nestmates, in particular, in initiating group attacks (Ayre 1968). In the ants of the group *F. rufa* these compounds act as attractants at lower concentrations, and induce alarm and attack behaviour at higher concentrations (Maschwitz 1964, Löfqvist 1976, Mabelis 1979b, Godzińska et al. 1991).

Protein demands of ant colonies and prey consumption are related primarily to the production of new individuals (among others, Ayre 1960, Lange 1960, 1962, Pętal 1968, Dlussky and Kupianskaya 1972, Kajak et al. 1972, Horn-Mrozowska 1976). Proteinic food is distributed preferentially to queens (which require proteins for egg production), to workers acting as nurses, and to developing larvae (among others, Le Masne 1953, Lange 1967, Vinson 1968, Markin 1970, Brian and Abbott 1977, Mabelis 1979b, Howard and Tschinkel 1981, Sorensen et al. 1981). In ant colonies presence of developing larvae stimulates the retrieval of animal prey (Haskins and Haskins 1950, Lappano 1958, Lange 1962, Mabelis 1979b, Wojtusiak et al. 1995). It may also modulate the choice of a hunting tactic (Wojtusiak et al. 1995).

Similarly as in other ant species, in the wood ants of the group *F. rufa* consumption of protein food is strongly related to the production of new individuals (Ayre 1960, Lange 1960, 1962, 1967, Mabelis 1979b). During the periods of scarcity of insect prey, these ants may even turn to cannibalism and exploit as food victims of intra-specific wars between neighbour colonies (De Bruyn and Mabelis 1972, Mabelis 1979b, 1984, Driessen et al. 1984).

In a laboratory experiment Lange (1962) demonstrated that hunting activity of *F. rufa* and *F. polyctena* is stimulated by the presence of larvae (in particular mature ones) and of queens preparing for egg-laying. Our recent research (Szczuka and Godzińska, in preparation) demonstrated, however, that in *F. polyctena* the readiness to retrieve insect prey may be retained also in absence of a queen and/or developing brood. We showed that workers of *F. polyctena* kept in laboratory continue to retrieve insect prey (dead houseflies) offered to them during the tests during relatively long periods (up to 10 months) even if they are kept in relatively small groups without queen and offspring. We also demonstrated that the expression of predatory/scavenging behaviour in such groups of workers was controlled in a crucial way by the size of the group. As a rule, retrieval of dead houseflies was retained only in groups composed of at least 30-40 workers. In groups composed of 20-30 workers the ants usually continued to seize and/or to transport the flies, but they did not retrieve them to their nests. Finally, in yet smaller groups, composed of less than 20 individuals, the responses of the ants to flies were limited mostly only to antennal contacts with the prey and/or to exploratory nibbling.

In the present experiment, we were monitoring the responses to insect prey (dead houseflies) in workers of *F. polyctena* kept in laboratory in small groups (initial size: 25 individuals) in absence of a queen and of offspring. These groups, the so called "derivative groups", were created by taking sets of workers out of larger groups, the so called "initial groups", also composed solely of workers, which were already kept in laboratory during five preceding months. Our derivative groups were created by selecting solely the workers belonging to a relatively uniform behavioural subclass, namely, those that responded to a dead prey item at least by persistent biting. Creation of such homogenous colony fragments with experimentally modified social structure was employed in very numerous studies devoted to the mechanisms underlying the division of labour in insect societies (among others, Lenoir 1979a, 1979b, McDonald and Topoff 1985, Lachaud and Fresneau 1987, Huang and Robinson 1992, 1996; see also the reviews of Lenoir 1987, Robinson 1992 and Stuart 1997). Wilson (1980, 1985a) called that technique the "pseudomutant technique", because thanks to it "the colony is modified by changing caste ratios, as though it were a mutant". The term "pseudomutant technique" was also used by some other myrmecologists, for instance, Herbers and Choiniere (1996). Splitting of the colony into homogenous fragments is also called the "sociotomy" (see, for instance, Lachaud and Fresneau 1987).

The results of our previous experiment suggested that in groups of workers of *F. polyctena* kept without a queen and developing larvae the threshold group size necessary for the long-term retention of the readiness to retrieve prey is approximately 30-40 workers. Hence, we predicted that in the derivative groups (counting each 25 individuals) the ants will cease to retrieve houseflies. We then intended to add gradually individuals to these groups to check whether this will result in the recovery of the retrieval of prey. In the present paper we report the results of the first part of that experiment, describing the dynamics of the disappearance of the readiness to retrieve prey in the derivative groups.

Similarly as in our first experiment, also now the responses of the tested ants to prey were investigated on the group level. Group/colony level of analysis is applied very frequently in recent experimental and theoretical studies of ant foraging behaviour (among others, Gordon 1987, 1988, 1991, 1992, Traniello 1987, 1989, Beckers et al. 1990, Traniello et al. 1991, Adler and Gordon 1992, Pacala et al. 1996). This is related, among others, to the fact that in social insects elements of behavioural sequences necessary to complete a particular task are often uncoupled and each of these elements is performed by a different individual (the phenomenon of the so called task partitioning; Jeanne 1986, 1991). In other words, the execution of multiple-step tasks is accomplished in the so called series-parallel sequence, a procedure known to result in a particularly high reliability of the system as a whole (i.e., a particularly high probability that the task will be completed) (Oster and Wilson 1978, Herbers 1981, Hölldobler and Wilson 1990).

The phenomena of task partitioning and/or cooperation between nestmates during hunting and scavenging for prey are well known also in the wood ants of the group *F. rufa.* It is known, among others, that wood ants often abandon their prey which is then taken over by another worker or a group of workers, that they may recruit nestmates to aggregations of prey, and that they may show competition for a prey item (among others, Chauvin 1950, 1968, Wellenstein 1954, Otto 1958, Sudd 1965, 1967, De Bruyn and Mabelis 1972, Büttner 1973, 1974a, b, c, Mabelis 1979b, Horstmann et al. 1982, Godzińska 1986, Godzińska et al. 1990, 1991, Sundström 1993). Hence, group level analysis of foraging behaviour of the "wood ants" - *F. truncorum* was recommended and employed already by Chauvin (1968). More recently, it was also used by Sundström (1993) in her analysis of foraging behaviour of *F. truncorum* Fabr.

METHODS

A large fragment of a colony of *F. polyctena* (composed of several thousands of individuals) was collected from a large nest belonging to a polydomous colony found in a pine wood near Krześlin (Siedlce District in Central-Eastern, Poland). The ants were collected together with a large amount of their nest material during two field trips, on 28 August 1991 and on 4 September 1991. They were transferred to laboratory in Warsaw and placed in a large formicarium in which they reconstructed a mound out of their original nest material. During the period 3-20 September 1991 we used these ants to create 22 groups composed of 20 to 1,200 workers. They were housed in open glass containers with the walls coated with Fluon (PTFE), a substance commonly used in the myrmecological research to prevent the ants from escaping from artificial nests by providing silky smooth surface. The ants were provided with the nest material taken from their original nest, which was promptly used by them to reconstruct small mounds. Water was provided in several large test tubes closed with tightly fitting cotton plugs. The ants were fed solely on honey mixed with crushed apples and with sand (added to make the mixture less sticky). No male brood production was observed in any of our groups during the whole experiment. During the period 9 October 1991 - 29 January 1992 we carried out a series of tests in which we investigated the responses of these ants to insect prey. On each test, a dead adult housefly was introduced into the tested nest. As a rule, the ants were not allowed to eat the fly: it was taken away after the end of the test, except when it was impossible to take it without damaging importantly the nest mound of the tested ants. Main results of this experiment are described briefly in the Introduction; they will be published separately (Szczuka and Godzińska, in preparation).

On 27-28 January 1992 we created the next generation of 24 experimental groups - the "derivative groups" - by taking sets of 25 workers out of nine "initial groups" tested in the previous experiment. Initially (in September 1991) the size of these nine "initial groups" ranged from 73 to 668 individuals; however, during the subsequent five months it gradually decreased, mainly as a result of worker mortality. As all dead ants were regularly removed and counted, we could monitor in a fairly precise way the modifications of the size of these groups resulting from the mortality of the ants. This method of estimating the number of surviving workers was fairly reliable because practically no cannibalism (consumption of dead nestmates) was observed in our experimental nests. In addition, in three nests some of the ants (altogether, 205 individuals) escaped. Thus, the total worker loss (resulting from both worker mortality and worker escapes) observed in our nine initial groups during five months preceding our present experiment was relatively high, reaching almost 60% of the initial number of workers. Worker mortality level observed in our colonies (about 12% per month) was similar to that observed in some other recent laboratory studies on *F. polyctena,* for instance, in the study of Czechowski (1996) mortality level in laboratory colonies of *F. polyctena* maintained on carbohydrate diet attained approximately 20% (18-21%) over the period of 3 weeks. However, according to Czechowski (personal communication), mortality level in laboratory colonies of *F. polyctena* is usually lower (43-60% over 8-9 months).

On 27 January 1992, immediately before the creation of the derivative groups, the estimated sizes of nine initial groups used as sources of workers for these groups were 30, 30, 40, 80, 100, 120, 150, 260 and 350 individuals, respectively. In all these initial groups the tendency to retrieve insect prey to the nest was retained until the end of the first experiment. Additionnally, each of these groups was checked for the presence of retrieval of the prey on the day before the creation of the derivative groups, and all these tests confirmed the retention of the full sequence of predatory/scavenging behaviour, terminated by the retrieval of the prey to the nest. These tests proved thus that relatively high mortality level in our initial groups did not affect the expression of predatory/scavenging behaviour in the surviving ants.

The derivative groups were created exclusively of workers which responded to a dead fly by at least persistent biting. To select and capture such workers, a dead housefly fixed to a thread was lowered into the foraging area of the nest housing the initial group. Only the ants which were biting the fly persistently enough to be taken out of their nest together with the fly when it was withdrawn were included into the set of individuals used to create the derivative group.

The derivative groups were housed in cylindrical glass jars (15-20 cm in diameter) with the walls coated with Fluon, in which they reconstructed small mounds out of their original nest material. The floor of each nest was covered by a thin (1-2 cm) layer of sand. The ants were fed and provided with water in the same manner as in their initial groups. They were exposed to natural rhythm of daylight/darkness supplemented every day from 9 a.m. to 9 p.m. by additional artificial white light illumination produced by four electric bulbs (two 200 W bulbs and two 100 W ones) placed close to the tested nests. Ambient temperature and relative humidity of the air (recorded in the close vicinity of the tested nests) were fairly stable (20-23°C and 42-50%, respectively). Similarly as in the initial groups, also now no male brood production was observed in any of our derivative groups during the whole experiment.

Our experiment was carried out during the winter and early spring, when in their natural environment the ants should have been hibernating. However, we did not break artificially the hibernation of our subjects, but we simply prolonged their activity by continuing to keep them at temperature conditions which allowed them to remain active. As all our groups were tested in parallel, any seasonal factors must have influenced the behaviour of our ants in the same way.

At the start of each test, a small (5 cm in diameter) Petri dish was pressed against the floor of the tested nest, and then during one minute we counted how many ants crossed the circular trace left by it on the sand. If no ant crossed that line, the ants of the tested group were considered to be inactive and the group was not tested on that day. If the ants were active, a dead adult housefly, killed by freezing and then defreezed, was placed in the middle of the circle traced by the Petri dish. From then on we recorded all responses of the ants to the fly until its retrieval to the nest. If the fly was not taken to the nest, the test was continued during 45 min. Immediately after each test the fly was removed from the tested nest. Then, we removed and counted all dead ants to monitor the modifications of the size of our groups resulting from worker mortality. Dead ants were removed after and not before each test to avoid a possible disturbing influence of that action on responses of the tested ants to the fly. On each test, we also recorded ambient temperature and relative humidity of the air in the close vicinity of the tested nest.

The derivative groups were tested for the first time within the first week after they had been created (3-5 days after their creation). Each group was then tested at approximately one week - ten day intervals until the disappearance of the retrieval of the flies, and then at least three times to check that there was no recovery of that behaviour. Thus, 14 groups in which the retrieval of the prey was absent already on their first test and never reappeared again were tested 4 times, 6 groups in which the retrieval of the prey was still observed on the second test were tested 5 times, and 4 groups in which the retrieval of the prey was retained up to the third test were tested 6 times. Intertest intervals ranged from 4 to 11 days (median: 7.5 days, lower and upper quartile: 6 and 10 days, respectively). Altogether, 110 tests were carried out.

The analysis of responses of the tested ants to houseflies was carried out on the group level. We analysed mainly the degree of completedness of the sequence of "predatory/scavenging behaviour attained by the tested group. The behaviour of the tested group was quantified as the value of the index D taking values in the following ordinal 1-6 scale:

1. inactivity of the tested group (no ant crossed the circle traced in the foraging area of the tested nest during 1 min);
2. antennal contacts (ant-prey interactions involved at the furthest antennal contacts of the ants with the prey);
3. nibbling (ant-prey interactions involved at the furthest prudent, hesitating biting of the prey, not followed by a typical attack behaviour);
4. biting (ant-prey interactions involved at the furthest biting of the prey, usually accompanied also by the contact of the ants legs and/or of the ventral surface of its body with the prey);
5. transport (ant-prey interactions involved at the furthest carrying/dragging of the prey, but without its retrieval to the nest mound);
6. retrieval (complete sequence of the predatory/scavenging behaviour, terminated by the retrieval of the prey into the nest mound).

Statistical analysis of our data involved Spearman rank correlation analysis of the correlations between, on one hand, D, and, on the other hand, (1) PDGS (= present derivative group size, i.e., the size of the derivative group on the day of the test, and (2) IGS (= initial group size, i.e., estimated size of the initial group of the tested ants immediately before the creation of their derivative group). To avoid the error of the so called pseudoreplication (cf. Machlis et al. 1985), we analysed separately the results obtained on each of the five tests. The results of the sixth test could not be analysed in this way, as only four groups were tested six times.

We also employed Spearman rank correlation analysis to test the correlations between IGS and the duration of the retention of the tendency to retrieve flies in the derivative groups. As our groups were tested at fairly variable intervals, we quantified the duration of the retention of the tendency to retrieve flies in the following three ways: (1) as the number of the successive tests during which the ants of that group continued to retrieve flies (NTR), (2) as the number of the days from the creation of a given group to the last test during which the ants were still observed to retrieve the fly (DR), and (3) as the number of the days from the creation of a given group to the first test during which the ants did not retrieve the fly (DNR).

Spearman rank correlation analysis was also employed by us to test the possible correlations between, on one hand, D, and, on the other hand, ambient temperature during the test (AT) and relative humidity of the air (RH). The correlations between D and AT were analysed only for the tests 3-5, as AT was constant (21°C) on the tests 1 and 2.

On each test we also recorded presence/absence of venom spraying. However, as venom spraying is not an obligatory element of the main sequence of the predatory/scavenging behaviour, we analysed its occurrence separately. The behaviour of the ants was quantified according to a binary scale (0 = absence, 1 = presence of venom spraying during the test).

To check whether the occurrence of venom spraying depended on the present derivative group size (PDGS) and the initial group size (IGS) of the tested ants, we compared the values of these indices for the groups in which the ants displayed venom spraying and for those in which venom spraying was not observed. These analyses were carried out by means of the two-tailed Mann-Whitney U test. They were made separately for each of the first three tests. The results of the fourth and the fifth test could not be analysed in this way, as on these tests venom spraying was observed only in 3 and 2 groups, respectively.

In a similar way, we also employed two-tailed Mann-Whitney U test to check the possible dependence of the readiness to display venom spraying on ambient temperature (AT) and relative humidity of the air (RH). In the case of AT, such analysis was made for the third test only, as AT was constant during the first two tests. In the case of RH, we analysed the results of the first three tests.

We also used Spearman rank correlation analysis to test the possible correlation between the survivorship of the ants in the derivative groups (quantified as their PDGS on the fourth test) and their initial group size (IGS).

RESULTS

The main results of our experiment are shown in Fig. 1.

As expected, in all derivative groups the ants fairly rapidly ceased to retrieve dead houseflies offered to them during the tests. From the fourth test on no retrieval of prey was anymore observed in any of our groups. Only in one case the ants were observed to transport the fly within the foraging area of their nest. During the whole experiment all tested ants retained, however, high level of general activity: they continued to explore actively foraging areas of their nests, and to respond to flies offered to them during the tests by displaying incomplete sequences of predatory/scavenging behaviour, limited to antennal contacts, nibbling, or biting. The tested ants were inactive only during 5 out of the total number of 110 tests (4.5 %) (Fig. 1).

Disappearance of retrieval of houseflies observed in the derivative groups was almost unexceptionally irreversible. As the only exception, the ants of the Group 10 (IGS = 120 individuals) retrieved the fly on their second

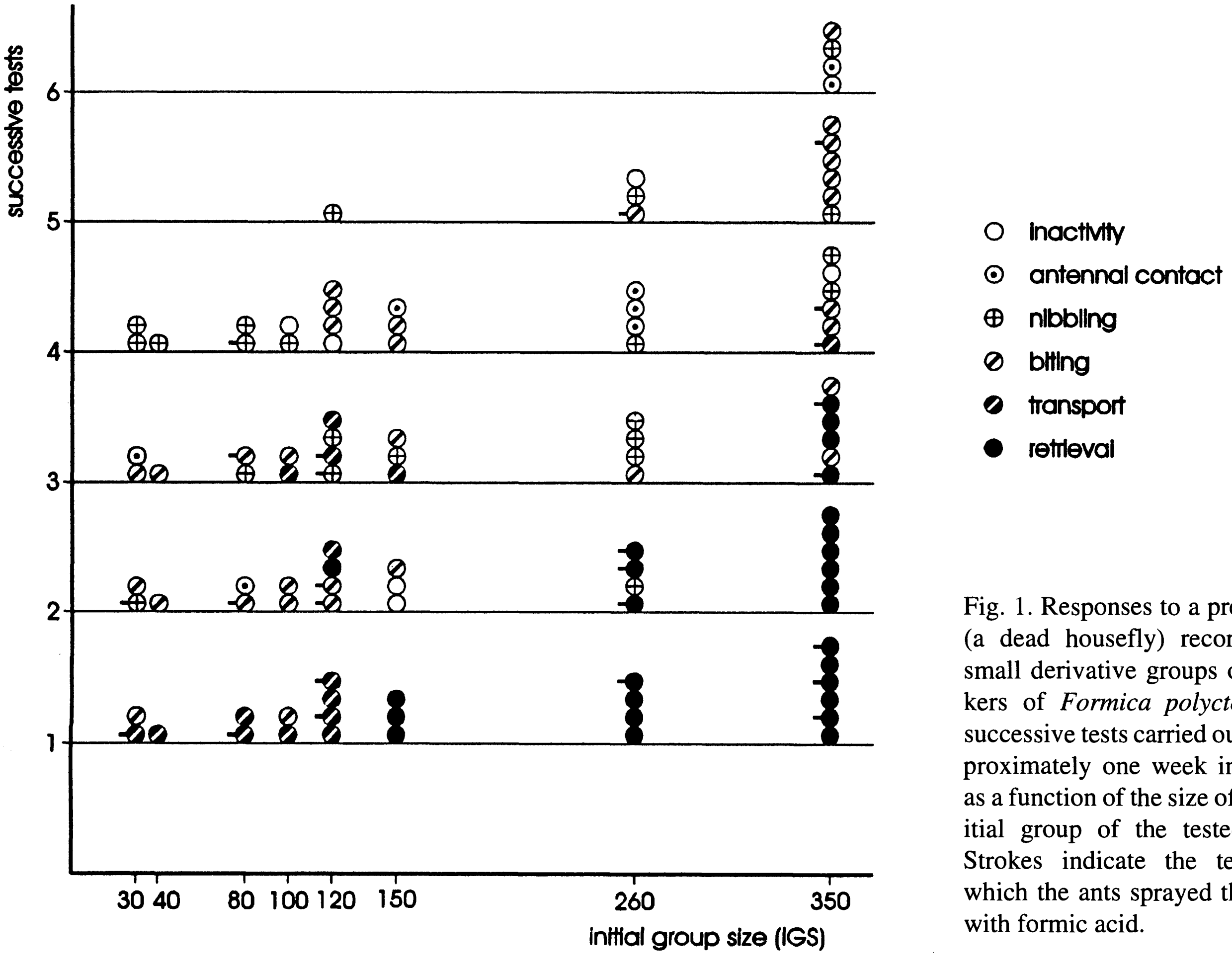

Fig. 1. Responses to a prey item (a dead housefly) recorded in small derivative groups of workers of *Formica polyctena* on successive tests carried out at approximately one week intervals as a function of the size of the initial group of the tested ants. Strokes indicate the tests on which the ants sprayed the prey with formic acid.

test, although they did not retrieve it on their first test (Fig. 1). However, the recovery of the complete sequence of predatory/scavenging behaviour observed in that group was transitory: from the third test on the ants of that group responded to flies only by nibbling or biting (Fig. 1).

As shown in Fig. 1, the duration of the period during which the ants of the derivative groups continued to retrieve flies was fairly variable. In almost a half of these groups (10 out of 24; 41.7 %) retrieval of the prey was absent already on the first test and never reappeared again. However, in 10 groups (41.7 %) the ants retrieved the fly also on their second test, and in 4 groups (16.7 %) they ceased to retrieve the fly only from the fourth test on.

Such variability in the duration of the retention of the readiness to retrieve prey in the derivative groups was unexpected by us. To account for that phenomenon, we sought for its possible causal factors. We started from analysing the possible effect of the present size of the tested group (PDGS). At the start of the experiment, all derivative groups were composed of 25 workers, but as a consequence of worker mortality their size decreased as a function of time (Table I). Therefore, we started from checking whether the values of D were correlated with the size of the group on the day of the test (= its present group size, PDGS). However, Spearman rank correlation analysis did not reveal any significant correlations between D and PDGS for any of the tests (Table I).

As the next step, we checked whether the values of D were correlated with the size of the initial group (IGS) of the tested ants as estimated immediately before the creation of their derivative group. This time, Spearman rank correlation analysis revealed highly significant positive correlations between D and IGS on the first two tests, and nearly significant correlations ($P<0.1$) on the third and the fifth test. Only on the fourth test D and IGS were not significantly correlated (Table I). These findings imply that in small groups of workers of *F. polyctena* the expression of predatory/scavenging behaviour depends not only on the present size of the group, as demonstrated by our earlier findings (Szczuka and Godzińska, in preparation), but also on its past size, and that these effects may be relatively long-lasting (up to several weeks).

To confirm these conclusions, we carried out yet another analysis to check directly whether the duration of the retention of the complete sequence of predatory/scavenging behaviour in the derivative groups is correlated with the size of the initial groups of the tested ants. As our groups were tested at variable intervals, we estimated the duration of the retention of the tendency to retrieve flies in each of them in three different ways (see Methods). As shown in Table II, the values of all these 3 indices proved to be highly significantly correlated with the size of the initial group of the tested ants.

Absence/disappearance of the retrieval of the houseflies observed in the derivative groups might have resulted from two factors: (1) changes in the motivational state of the surviving workers, and (2) absence/elimination of the workers which specialized in the retrieval of prey. To create the derivative groups, we used exclusive-

TABLE I

The results of the Spearman rank correlation analysis of correlations between the degree of completedness of the sequence of scavenging behaviour (D) observed in small groups of workers of *Formica polyctena* on five tests carried out on successive weeks, and the present and past size of these groups. PDGS = present size of the tested group. IGS = size of the initial group of the tested ants. D took values in an ordinal 1-6 scale. For further explanations see the text

			Correlations of D with PDGS		Correlations of D with IGS	
Test	No. of tested groups	PDGS (range)	Correlation coefficient (ρ)	Probability level (*P*)	Correlation coefficient (ρ)	Probability level (*P*)
1	24	22 - 25	-0.0937	0.6533	0.8733	< 0.0001
2	24	19 - 25	0.1750	0.4014	0.7776	0.0002
3	24	18 - 25	- 0.1872	0.3692	0.3918	0.0602
4	24	12 - 24	0.2515	0.2277	0.0118	0.9548
5	10	10 - 24	- 0.2485	0.4560	0.6151	0.0650

TABLE II

The results of the Spearman rank correlation analysis of correlations between various parametres quantifying the duration of the retention of the complete sequence of scavenging behaviour observed in small groups of workers of *Formica polyctena* and the size of the initial groups of the tested ants. NTR = number of successive tests during which the ants continued to retrieve flies. DR = time (in days) from the creation of the derivative group to the last test during which the ants were still observed to retrieve the fly. DNR = time (in days) from the creation of the derivative group to the first test on which the ants did not retrieve the fly. IGS = size of the initial group of the tested ants. For further explanations see the text

Correlation between	Correlation coefficient (ρ)	Probability level (*P*)
NTR and IGS	0.9312	< 0.0001
DR and IGS	0.8824	< 0.0001
DNR and IGS	0.9057	< 0.0001

ly the individuals that were responding to the prey by persistent attack, but there remains a possibility that they did not specialize in the retrieval of prey to the nest as well. The elimination of the workers specializing in the retrieval of prey might also have occurred already after the creation of the derivative groups, as a result of worker mortality.

To throw more light on that question, we checked whether in any of our derivative groups the retrieval of the prey was present on the first test (or tests) and then disappeared in spite of the fact that no ant died. In a such group disappearance of the retrieval of the houseflies could not have resulted from the elimination of workers which specialised in the retrieval of prey: it must have resulted only from some modifications in the motivational state of the workers belonging to that group. We discovered two such cases: Group 5 (IGS = 350 individuals), and Group 7 (IGS = 260 individuals). In both these cases, all 25 ants used to create these groups survived during the first three tests. Nevertheless, in both these groups the ants retrieved the fly only on the first two tests: on their third test ant-prey interactions were limited to biting the fly (Group 5) or to nibbling it (Group 3). Hence, at least in these two cases the disappearance of retrieval of the prey could have resulted exclusively from some change(s) in the motivational state of the workers belonging to the tested groups.

None of the analysed correlations between D and ambient temperature (AT) were significant (Spearman rank correlation analysis: always NS). This was not surprising, as AT was very little variable (ranging from 20 to 23°C).

Significant correlation between D and RH was discovered only in one case, for the fourth test (Spearman rank correlation coefficient = 0.5370, *P*=0.01). However, this single case does not allow us to conclude that the differences in the behaviour of the ants really reflected the differences in the relative humidity of the air, as no such correlation was discovered for any other test (Spearman rank correlation coefficient: always NS), and as on the fourth test RH was very little variable (ranging from 45% to 48%). Moreover, RH was very little variable throughout the whole experiment, ranging from 42 to 50%.

We also analysed factors influencing the occurrence of spraying the prey with the formic acid (= venom spraying). That behaviour was clearly facultative: it was recorded only on 25 out of the total number of 110 tests (22.7 %). It was always preceded by biting or at least by nibbling of the prey.

To check whether the occurrence of venom spraying depended on the present size of the derivative groups (PDGS) and on the initial group sizep size of the tested ants (IGS), we compared the values of these indices for the groups in which the ants displayed venom spraying and for those in which venom spraying was not observed. Only the data for the first three tests were analysed in that way, as on the other tests venom spraying was too little frequent (see Fig. 1 and Methods). As shown in Table III, on the first and on the third test the present size (PDGS) of the groups in which the ants displayed venom spraying was significantly smaller than in the case of the groups in which the ants did not display that behaviour. In contrast, the values of IGS of these groups did not differ significantly on any of the three tests (two-tailed Mann-Whitney U test: NS for all three tests).

No significant differences were discovered in any of the analyses comparing the values of ambient temperature (AT) and relative humidity of the air (RH) recorded during the tests on which the ants displayed venom spraying and during those on which venom spraying was not observed (two-tailed Mann-Whitney U test: always NS).

The survivorship of the ants in the derivative groups (quantified as their PDGS on the fourth test) was not correlated with their initial group size (IGS) (Spearman rank correlation analysis: NS).

TABLE III

The values of the present group size (PDGS) of the derivative groups in which the ants sprayed the prey with the formic acid (= venom spraying present) and of those in which the ants did not display that behaviour (= venom spraying absent) on three first successive tests. Statistics: two-tailed Mann-Whitney U test. For further explanations see the text

Test	PDGS (median ± range)		Probability level (*P*)
	Venom spraying present	Venom spraying absent	
1	25 (22-25)	25 (25-25)	0.0225
2	23.5 (21-25)	24 (19-25)	NS
3	18 (18-21)	23 (19-25)	0.003

DISCUSSION

Our present data, together with the results of our earlier experiment (Szczuka and Godzińska, in preparation) demonstrate that the responses of workers of *F. polyctena* to dead insect prey may depend in a crucial way on the size of the group. As already told in the Introduction, our earlier experiment (Szczuka and Godzińska, in preparation) showed that the expression of the full sequence of predatory/scavenging behaviour terminated by the retrieval of prey to the nest may be retained in a group of workers of *F. polyctena* also in absence of queen and of brood, but only if the group is larger than the "threshold size" of 30-40 individuals. Our present data confirmed that conclusion: in all our derivative groups (composed of 25 or less individuals) the ants ceased to retrieve insect prey.

As discovered by Wilson (1984, 1985a), ant workers may respond to modifications of the colony structure by the expression of formerly silent behavioural programmes in a very rapid way (within an hour). These rapid effects are to a large degree reversible. In contrast, in our present experiment the effect of group size on the expression of scavenging behaviour in groups of workers of *F. polyctena* did not consist simply in switching that behaviour off when the group size fell below a certain threshold. In our case the expression of scavenging behaviour depended not only on the present group size, but also on the history of the group: the duration of the retention of the expression of the complete sequence of scavenging behaviour was positively correlated with the past size of the tested groups before their reduction to the uniform level of 25 individuals. These effects of past group size were relatively long-lasting: in some of our derivative groups they were retained during several weeks.

Our present data imply thus that the influence of the size of the group on the expression of predatory/scavenging behaviour in workers of *F. polyctena* is characterized by a fairly important inertia, which in turn suggests that that influence is exerted in an indirect way. Hence, one of the possible hypothetical explanations of our present data is that some external factor(s) related to the group size influence(s) in these ants the level of some internal factor(s) I, which in turn control(s) the expression of predatory/scavenging behaviour.

In our first experiment (Szczuka and Godzińska, in preparation) the values of the index D quantifying the degree of completedness of the sequence of predatory/scavenging behaviour were correlated positively with the size of the group. However, D was not a linear function of group size: as a rule it attained its ceiling value of six already when the group size attained the level of 30-40 individuals. The results of our present experiment suggest that in workers of *F. polyctena* the level of the hypothetical internal factor(s) I controlled by the size of the group (and controlling in turn the expression of predatory/scavenging behaviour) continues to increase with the increasing group size also in groups composed of more than 30-40 individuals, although in such groups the increase of I can be no more reflected in the increase of D. To explain fully the main effect observed in the present experiment - the positive correlation between the duration of the retention of the complete sequence of predatory/scavenging behaviour and the past size of the tested group before its reduction to 25 individuals - we must also make an additional assumption that after the reduction of the group size to the level of 25 individuals the level of the factor I decreases with time at the rate which does not depend on the initial size of the group.

The above hypothesis concerning the proximate mechanisms of the effects observed in our present experiment is open for further research, and other alternative explanations of our results are also possible. However, we already demonstrated that at least in some of our derivative groups disappearance of the full sequence of predatory/scavenging behaviour did not result solely from absence/elimination of workers which specialised in the retrieval of the prey, but involved some modification(s) in the motivational state of the surviving workers (see Results). This conclusion was further supported by the results of our next experiment, carried out immediately after the end of the present one. In that experiment we gradually increased the size of ten of our derivative groups by adding to each of these groups workers taken from the remaining derivative groups. The retrieval of houseflies reappeared again in all these groups once they have reached a sufficient size (Szczuka and Godzińska, in preparation). These findings demonstrated thus that the modifications in the motivational state of workers of *F. polyctena* induced by very small group size are reversible. They also supported further our conclusion that the disappearance of the readiness to retrieve prey observed in our present experiment was caused indeed by the modifications of the group size, and not, for instance, by a possibly deteriorated general state of our subjects related to relatively high mortality level observed in our groups, or by the possible effects of the carbohydrate diet on which were maintained our ants. Anyway, in the ants of the group *F. rufa* food deprivation and purely carbohydrate diet are known to stimulate and not to suppress the readiness for hunting and retrieval of animal prey (Büttner 1974c, Horstmann 1975, Mabelis 1979b).

The hypothesis postulating that in *F. polyctena* the expression of scavenging behaviour is controlled *via* some internal factor(s) I which is in turn controlled by the size of the group is also indirectly supported by many data demonstrating the existence of similarly acting factors in many insect species. In particular, in many insects, including social Hymenoptera, the expression of various behavioural traits is controlled by the level of the juvenile hormone (for the reviews, see Robinson 1992, Fahrbach and Robinson 1995; see also Stout et al. 1991, 1992 and Wallikonis et al. 1991 for the data concerning the influence of the juvenile hormone on the expression of behaviour in a non-social insect species). In groups of worker honeybees (*Apis mellifera* L.) both the juvenile hormone level and the expression of various behavioural traits may be influenced in a crucial way by the size of the group (Huang and Robinson 1992).

In the ants, the size of the group may also influence the level of certain brain neurotransmitters. As shown by Kostowski et al. (1975), workers of *F. rufa* taken out of a large formicarium and isolated in a small group of 10-12 individuals showed small but statistically significant increase in the brain level of serotonin already after an hour of isolation. As shown earlier by Kostowski and Tarchalska (1972), in workers of that species serotonin injections led to a significant decrease of the readiness to attack a large insect (a beetle of the genus *Geotrupes*), accompanied by increased mutual aggressivity between the nestmates aggregating around the prey. Kostowski et al. (1975) also demonstrated that any type of the attack (directed to a beetle or directed to a nestmate) is followed in these ants by a significant increase in the brain level of serotonin. All these data suggests that serotonin may play an important role in the control of the expression of predatory behaviour in the ants of the group *F. rufa*.

Our present data suggest strongly that in very small groups of workers *of F. polyctena* (composed of 25 or less workers) the readiness to display venom spraying tends to increase with the decreasing size of the group. This finding supports additionally our conclusions concerning the importance of group size in determining the character of responses to prey shown by *F. polyctena.* As pointed out by Wilson (1971) and Oster and Wilson (1978), the loss of a worker is more detrimental for a small social insect colony than for a large one. Hence, Oster and Wilson (1978) and Herbers (1981) predicted that workers from small colonies should be relatively more risk-averse than workers from larger ones: in particular, they should move more slowly and to behave more circumspectly, so as not to overlook food items or to over-expose themselves to predation. In other words, the overall activity level of workers, the so called tempo, should be positively correlated with the colony size.

Experimental research carried out to test that hypothesis (Leonard and Herbers 1986, Herbers and Choiniere 1996) so far did not yield concluding results, as in both these studies the number of tested colonies was relatively small, and the results of the experiments were to a large degree contradictory.Our present data support to some degree the predictions of Oster and Wilson (1978) and Herbers (1981) postulating the existence of a negative correlation between the colony/group size and the level of the risk-aversiveness of its members. The decreased readiness to retrieve animal prey and the increased readiness to display venom spraying observed by us in small groups of workers of *F. polyctena* may be both interpreted in terms of the colony level response to a decrease in the colony size designed to reduce the risk of further worker loss. As already told, venom spraying occurs in the formicine ants among others as the element of the so called prudence behaviour, displayed in response to large or potentially dangerous prey (Dejean 1988, Dejean et al. 1994). Increased readiness to display venom spraying in response to dead prey items observed by us frequently in particularly small groups of workers of *F. polyctena* may thus be related to the lowering of the threshold for the "prudence behaviour". However, we would like to stress that the effects of the group size on the readiness to display venom spraying observed in our experiment were relatively weak: they were observed only on the first and the third test. On the last two tests venom spraying was very rare, although the values of the present group size continued to decrease as the result of worker mortality. Therefore, our present data concerning the relationship between group size and readiness to display venom spraying in *F. polyctena* cannot be considered as conclusive.

The role of colony/group size in controlling various features characterizing foraging behaviour of social insects was discussed in many theoretical studies (among others, Meyer 1966, Oster and Wilson 1978, Herbers 1981, Houston et al. 1988, Jaffe and Deneubourg 1992). In a synthetic paper, Beckers et al. (1989) reviewed very numerous literature data concerning the relationship between the size of the colony and the type of foraging system in the ants. These data support the hypothesis of the authors that the degree to which the behaviour of individual foragers is coordinated by chemical communication increases with the increasing colony size. Ant colony size may also influence patterns of food distribution between workers (Howard and Tschinkel 1980), the proportion of ants engaged in foraging (Mirenda and Vinson 1981), and the so called foraging tempo (Leonard and Herbers 1986, Herbers and Choiniere 1996). It has also been shown recently that the ants may use the rate of contacts with their nestmates as means of assessing their density (Gordon et al. 1993), and that they may modify many features of their searching and foraging behaviour in response to the density of their nestmates (Gordon 1995, 1996).

The relationship between the colony size and the presence/absence of predatory/scavenging behaviour was studied mainly in incipient (newly founded) ant colonies. First generation workers as a rule avoid danger and hence they do not hunt (Wilson 1971, Oster and Wilson 1978, Dejean et al. 1989, Dejean et Lachaud 1994). In *Polyrhachis laboriosa* F. Smith, an African formicine species, the expression of the complete sequence of hunting behaviour appears only in workers from polydomous colonies: workers from smaller colonies respond to potential prey by escape, avoidance, or at the furthest abandon them at the stage of attack (Dejean et al. 1994). Similar situation is also observed in another African formicine, *Oecophylla longinoda* Latreille: workers from small colonies do not hunt, and retrieval of very large prey items is observed only in very large polydomous colonies (Wojtusiak et al. 1995).

In incipient ant colonies colony size usually covaries with its age and it is often extremely difficult to dissociate the effects of these two variables (Wilson 1983, 1985a, b, Herbers and Choiniere 1996). In contrast, in our present experiment we could investigate the effects of group size in an experimental situation in which the possible effects of factors related to colony age were greatly reduced, and the effects of stimulation produced by the queen and brood were absent. Our experimental model enabled us to dissociate the effects of group size from the effects of colony age and from the effects of factors related to the presence of queen and brood, which is impossible in studies using incipient colonies.

Literature data on responses to prey shown by ant workers kept in laboratory without queens and brood do not present a uniform picture. For instance, in a laboratory experiment of Horn-Mrozowska (1976) workers of *Formica pratensis* Retz. kept without offspring in queenright groups of about 100 workers did not eat any proteinic food offered to them in form of housefly larvae and meat. However, in the experiments of Brian (1973) workers of *Myrmica rubra* L. kept in groups of about twenty without queens and larvae were eating adult fruit flies offered to them, although in such groups consumption of prey was lower than in groups containing larvae and/or queens.

In the ants of the genus *Formica* the effects of colony/group size on the expression of predatory/scavenging behaviour were so far not known. However, several studies investigated in these ants the effect of colony size on the consumption of prey. Interestingly, prey consumption did not always increase as a function of the colony size. In the study of Ayre (1966), consumption of insect prey per individual recorded in queenright laboratory colonies of *F. polyctena* Förster and *F. exsectoides* Forel (size range: 300 - 4,800 workers) depended on the size of the colony in a different way for each tested species. Whereas *F. exsectoides* consumed proportionally more prey in larger colonies (composed of more than 1,300 workers) than in smaller colonies, the reverse was true for *F. polyctena*. As shown by Cherix (1987), foragers of a relatively small polydomous colony of *F. yessensis* Forel (composed of 13 nests only) retrieved prey items much more frequently than the foragers of a very large super-colony composed of a system of about 45 thousands interconnected nests.

In the ants of the group *F. rufa*, colony/group size controls not only various features of foraging behaviour, but also other processes. Colonies of these ants can produce sexuals only if they attain a particular threshold size (Gösswald and Bier 1954, Chauvin 1969, 1972).

An interesting parallel to our present results can be found in the study of Skibińska (1982) devoted to various factors influencing the level of aggressivity shown by workers of *F. exsecta* against alien conspecifics. In that laboratory study, workers of *F. exsecta* displayed aggressivity against alien conspecific workers only if they belonged initially to a monogynous field colony, and if they were then kept in laboratory in a colony which was both queenright and composed of at least 250-300 individuals. In smaller colonies workers were not aggressive against alien conspecific workers. Skibińska also observed that within 48 h after the removal of the queen orphaned workers *of F. exsecta* stopped to be aggressive against alien conspecific queens. However, in the case of particularly aggressive colonies workers continued to respond to alien queens by milder forms of aggressive behaviour during longer periods. Aggressivity of orphaned workers of *F. exsecta* against alien conspecific workers was retained during much longer periods ranging from several days up to 20 days. The duration of the period during which the workers of an orphaned colony retained their aggressivity against alien conspecific workers was higher in colonies which were more aggressive while they were still queenright. As can be seen, the phenomena described by Skibińska in *F. exsecta* are strikingly similar to those reported by us presently for *F. polyctena*.

As pointed out in several recent papers (for instance, Gordon et al. 1992, Herbers and Choiniere 1996), in ant species in which polygynic nests split seasonally into smaller units and then merge again into larger colonies (the phenomenon of the so called "seasonal polydomy") the same individual workers may live in groups of various and varying size during their lifetime. The phenomenon of seasonal polydomy is widespread among ants, including the ants of the group *F. rufa*; moreover, in polydomous colonies of the ants of that group workers often move from nest to nest, or are transported to another nest by their nestmates (Rosengren 1971, 1985, Pisarski 1982, Mabelis 1979a, 1979b, Pętal 1980, Rosengren and Pamilo 1983, Czechowski 1984, Rosengren et al. 1985, Gordon et al. 1992). Experimental data concerning the effects of group size on ant foraging behaviour may thus throw some light on the proximate mechanisms underlying ant foraging in the field (Herbers and Choiniere 1996).

In our present experiment, the behaviour of the ants was not influenced in a significant manner by ambient temperature, nor by relative humidity of the air. Absence of such effects resulted undoubtedly from very narrow variability range of these two meteorological factors. Temperature conditions are known to influence in a significant way predatory activity and various features of hunting behaviour of *F. polyctena* (among others, Horstmann 1970, Büttner 1974a, Mabelis 1979b). In contrast, according to Büttner (1974a), relative humidity of the air had no effect on predatory behaviour of *F. polyctena* in laboratory.

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