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Recruitment signals and raids in slave-maker ants

[With 20 Text-figures]

Introduction

Predatory expeditions of ants of the subgenus *Raptiformica* FOR. and genus *Polyergus* LATR. to the nests of other ants in search of larvae and pupae, the so-called raids, represent one of the forms of social parasitism. The raids are organized actions involving hundreds or even thousands individuals, so they need an extremely well developed and precise communication system. This feature distinguishes the raids from other activities of social insects. The best known European ant species which are social parasites grabbing offspring of other species are *Formica* (*Raptiformica*) *sanguinea* LATR. and *Polyergus rufescens* LATR. Social parasitism in *F. sanguinea* is not obligatory, and frequently their "pure" societies can be met, while *P. rufescens* is an obli gatory parasite, always occurring in mixed swarms, and incapable of self-dependent existence.

The slave-making instinct has probably been developed in ants as the effect of a peculiar food specialization, i. e., due to grabbing offspring from the nests of other species for food. This suggestion is based on the fact that a considerable part of prey is used as food in *F. sanguinea* and *P. rufescens* colonies (DOBRZAŃSKI 1965, CZECHOWSKI 1975a, b, c).

It is supposed, and partly proved in some experiments, that chemical signals in the form of pheromones excreted by the workers stimulate *Raptiformica* and *Polyergus* to raids. Respective biochemical data are known only for the species living in North America: *Formica pergandei* EM. and *Formica subintegra* EM. of the subgenus *Raptiformica* (REGNIER and WILSON 1971, WILSON 1975) and *Polyergus lucidus* MAYR (TALBOT 1967). These ants, however, are so closely related to the corresponding Palaearctic species that the results can be referred to them as well. The development of pheromone signals was possible due to the formation of special glands producing chemical compounds of complex structure and specific activity, or due to the adaptation of glands already existing to new function. Such complicated evolutionary changes must have taken much time during the phylogenesis of *Raptiformica* and *Polyergus*. So, it may be expected that they had occurred before the main line of descent began to differentiate into the forms inhabiting particular zoogeographic regions.

Production and excretion of pheromones are particularly well developed in ants organizing predatory expeditions, as compared with other species. The Dufour glands, one of the main organs producing pheromones in ants, are many times larger in *F. pergandei* and *F. subintegra* than, for example, in the workers of *Formica* (*Serviformica*) *subsericea* Say which are frequently met as "slaves" in the nests of North American species of *Raptiformica* (Regnier and Wilson 1971, Wilson 1975).

The effect of pheromones can be revealed in three situation types corresponding to successive phases of a predatory expedition:

1 — mobilization of the swarm before an expedition;

2 — maintaining a proper itinerary;

3 — battle against the defenders of the attacked colony.

1. So far, there are no data on the recruitment signals in ants which are social parasites, and the nature of these signals can be deduced from the behaviour of ants in the preliminary phase of the expedition.

2. Maintaining of the proper itinerary by the columns of *F. pergandei*, *F. subintegra* or *P. lucidus* is controlled by trail pheromones laid down by scouts to trace the way from an object found to their own nest (Regnier and Wilson 1971, Wilson 1975, Talbot 1967). But also the raids not preceded by scouting and without pheromones marking the way are possible, at least in the European species *P. rufescens* (Dobrzańska and Dobrzański 1960, Czechowski 1975b).

3. During the battle the workers of *F. pergandei* and *F. subintegra* excrete alarm pheromones encouraging them and, at the same time, having a discouraging effect on the defenders of the attacked colony (Regnier and Wilson 1971, Wilson 1975). There are no data on the effect of respective pheromones at this phase in ants of the genus *Polyergus* as yet.

In this paper the observations, conclusions and hypotheses concerned with recruitment signals are presented and also with other ways of information exchanges in European ants making slaves, such as *F. sanguinea* and *P. rufescens*.

Study area and subject

Aggressive behaviour of *F. sanguinea* was studied in the Bieszczady mountains at Berezki, located near Ustrzyki Górne, in 1970–1972, and at the edge of the Kampinos Forest at Łomna-Las near Warsaw, in 1973. In the Bieszczady mountains aggressive behaviour of *F. sanguinea* was observed towards other species the colonies of which were experimentally established near their nests. In the Kampinos Forest natural situations were observed, such as an attack of *F. sanguinea* swarm upon a polycalic colony of *Formica* (*Serviformica*) *cinerea* MAYR, and the behaviour of *P. rufescens* coexisting with *F. cinerea* workers kept as "slaves", and organizing predatory expeditions to neighbouring colonies of *F. cinerea* and *Formica* (*Serviformica*) *fusca* L.

Terminology

As there are considerable discrepancies in myrmecological terminology used by different authors, the terms used in this paper are listed below:

nest – the construction made and inhabited by ants;

ant-hill – the aboveground part of a nest of ants of the genus *Formica*, made up of organic remains;

swarm – all ants (workers, sexuals, offspring) inhabiting a nest;

colony – a nest together with the swarm in it;

branch – a filial colony formed as the result of the division of a maternal swarm;

polycalic colony – a community of the colonies of common origin, which are in touch with each other;

society – all ants inhabiting a single (monocalic) nest or a community of nests forming a polycalic colony. In the case of a monocalic colony the term "society" corresponds to the term "swarm";

artificial colony (branch), experimental colony (branch) – a colony experimentally established in a selected place.

Methods for establishing artificial colonies

The nests of *Formica exsecta* NYL. and *Formica pressilabris* NYL. of the subgenus *Coptoformica* MÜLL., and *Formica pratensis* RETZ. of the subgenus *Formica* L. s. str. were experimentally established near the nests of *F. sanguinea*. Under natural conditions these three ant species are not usually "slaves" in *F. sanguinea* societies but for many reasons they are easy to experimental colonization and they support it well. Due to a large ethological plasticity of *F. sanguinea* this fact is not an effective difficulty in carrying out experiments.

The technique of experimental colonization of ants constructing nests with the aboveground part in the form of a mound composed of organic remains is very simple, at least when relatively short-term observations are conducted (this problem is much more complex when ant colonization is used as a biological method for forest protection). To move a colony, or in fact a part of it, a certain amount of nest material with the possible highest number of workers, larvae and pupae is taken from the ant-hill and put in an appropriate place. The branches were transported in high plastic containers with inner edges wetted with the paraffin oil. When polyginic societies are moved, the branches from several colonies may be joined, and swarms can be reinforced by workers and offspring taken from other societies. If the branch is taken on a warm, sunny day, it is possible to get some females (from a polygynic society). The presence of a female in the artificially established colony is not necessary if the experiment lasts no more than a season. The behaviour of workers from swarms without females does not deviate from normal one, at least from the outside, only the existence of such colony is limited in time.

When new colonies are artificially established, the most important problem is to find an appropriate habitat, not very different from a typical one. Otherwise ants move from the selected site within a short time, frequently to distant places. Also the weather conditions are very important on the day of transport and during some successive days afterwards till the time when the new colony reaches a certain stability. Some warm days without rain are also needed to restore the damage to the maternal nest caused during taking the branch.

Artificial nests were established within the territories of *F. sanguinea* at different distances from their nests. When a new-established nest was located too close to a colony of *F. sanguinea* and not separated from it by any natural screen, it was generally attacked and totally destroyed before it could reach any stability in the new place. In this situation the course of the conflict could not be regarded even as a similar to natural one. To prevent this, some particularly threatened new colonies were temporarily separated from the area of *F. sanguinea* by means of 20-cm high fences made of long celluloid bands partly sinked into the ground and supported by sticks fastened in the ground. The upper edge of the fence was oiled with paraffin which forms an impassable zone for ants. But these measures were not always effective. A new component suddenly appearing within the nest territory attracted a number of *F. sanguinea* searching the area, and even a small crevice in the fence was enough to attack the intruders.

Recruitment and raids in *Formica sanguinea*

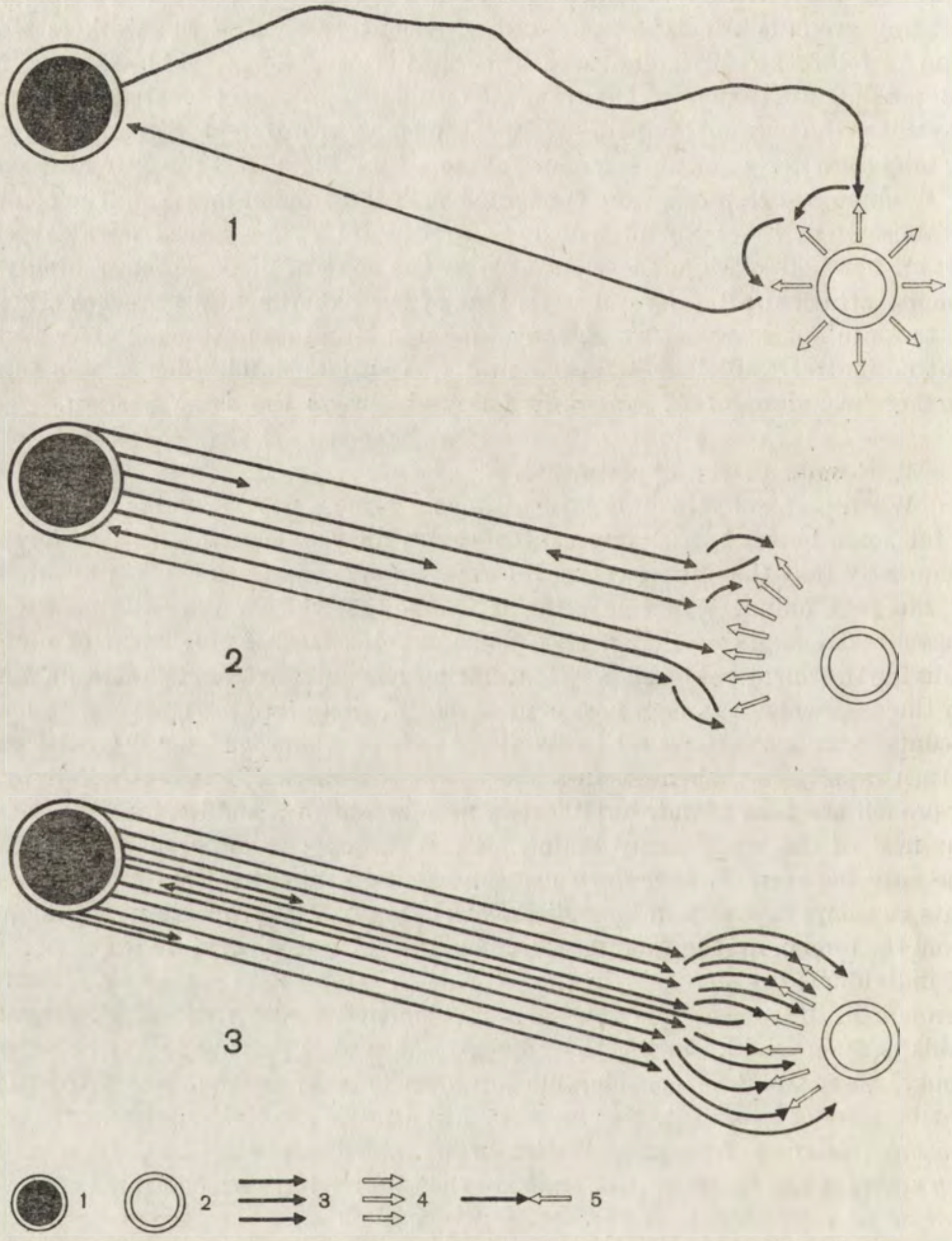
Relationship between a *F. sanguinea* society and an artificial colony of another species can be regarded as a model of the natural system including a social-parasite society and newly detected slave-species society. Therefore, the experimental situation may be compared to that when *F. sanguinea* workers searching the area encounter for the first time a foreign nest under natural conditions. But such individuals can not be called scouts literally as foreign nests in this species are located to some extent "by chance" by individual *F. sanguinea* foragers searching for food. It seems that there is no special functional group of individuals specialized in searching for reserve "slaves" (DOBRZAŃSKI 1961).

Members of *F. sanguinea* societies are characterized by a special way of searching the territory around the nest as they have the so-called "elongated foraging grounds". This is the result of a conservatism of the workers which tend to follow already frequented directions (Dobrzański 1961). Thus, to find the possible differences in the response of ants to an object located at different positions, the artificial colonies were established in different directions around *F. sanguinea* nests and at different distances from them. But the only differences in *F. sanguinea* response were concerned with the time of location. The colonies established in the zone intensively searched by *F. sanguinea* were attacked within few hours, while those situated in the zone of dispersed searching were usually attacked after several days. One of the experimental branches situated in the site not searched by *F. sanguinea* was found and attacked after a year. But no matter where the attacked nest was situated and when it was found, further behaviour of *F. sanguinea* followed always the same pattern.

1. Results of the experiments.

When a *F. sanguinea* individual finds a foreign nest, it walks close around it for some minutes, avoiding conflicts with ants which attack it. It happens frequently that the ant collecting information is captured and killed by workers of the nest found. When scouting is completed, the *F. sanguinea* individual goes directly to its nest (Fig. 1). A considerable speed of movement of such an individual, considerably higher than during normal searching, should be noted. In the case when a foreign nest is near to a *F. sanguinea* nest, several "pseudo-scouts" can gather around it. While a part of them go round it, the other return rapidly to their nest. In a short time still more *F. sanguinea* individuals approach the nest found, but there is no moment of a sudden emergence from the nest of the whole army taking part in the expedition. Density of ants on the way between *F. sanguinea* nest and foreign nest increases gradually, and ants go along this way in both directions (Fig. 2). The proportion of ants going from the foreign nest to their nest decreases with time, when still greater numbers of individuals are involved in the expedition. But till the end of the conflict, through all its phases the two-sides movement characteristic of *F. sanguinea* raids is maintained. During the battle, besides ants coming to their nest with booty, there are also considerable numbers of ants without booty, certainly, not because of lack of it. Nor are they less sensitive individuals which for some reasons "resigned" from participation in the raid. Their behaviour, and especially the speed of their movements, indicate that they have a special role in the raid. It can be suggested that the apparently useless ants running along the trail in both directions mobilize the swarm or, at least, they maintain an appropriate level of stimulation in the remaining part of the army.

North American ant species of the subgenus *Raptiformica* excrete alarm pheromones activating the army of aggressor during the flight (Regnier and Wilson 1971, Wilson 1975). Such signals certainly occur also in *F. sanguinea.*



Figs 1–3. Mobilization and the first phases of the predatory expedition of *F. sanguinea* to the experimental colony of *F. exsecta*: 1 – *F. sanguinea* nest; 2 – artificial nest of *F. exsecta*; 3 – movement of *F. sanguinea*; 4 – movement of *F. exsecta*; 5 – fight. (Description in the text).

Thus, it is possible that the role of individuals involved in the raid but not participating in grabbing lies in the formation of a kind of "pheromone tunnel" along the way of the raid to maintain or increase the state of stimulation in ants already involved. On the other hand, the behaviour of these ants is similar to the response of "pseudo-scouts" returning to their nests to inform the society about the nest found. So, it is also possible that they perform a similar function, i. e., they provoke less sensitive individuals still remaining in the nest to march out. These individuals are also likely to restore permanently odour trails laid by the first individuals which found the nest attacked, of course, if marked ways of this kind exist in the case of *F. sanguinea* raids, as it has been found in *F. pergandei* and *F. subintegra* (Regnier and Wilson 1971, Wilson 1975). So, at the moment, the role of ants which can be called "signallers" is not clear.

F. sanguinea individuals gather in still increasing numbers at a short distance from the foreign nest, they outflank it semicircularly (occasionally they surround it), and initially they avoid fights with alarmed defenders of the threatened nest (Fig. 2). In this phase of the conflict, the fights among the adversaries are rare, and they are generally initiated by inhabitants of the invide nest. But this phase is short and it is followed by a violent attack upon the surrounded colony (Fig. 3). All successive phases of the aggressive behaviour of *F. sanguinea* army follow smoothly, without sharp boundaries. Also the transition from the state of siege to the state of a violent attack is not abrupt. The change in the situation, however, is so rapid in this case that the moment of the concentrated attack is almost conspicuous. Thus, it may be suggested that it is produced by a definite stimulus. It may be the effect of an concentration of alarm pheromones in the air, which reaches a threshold value with increasing number of invaders. While the ants which first attacked the nest contain considerable forces of defenders, newly arrived individuals from more distant ranks invide the nest and grab larvae and pupae. *F. sanguinea* workers continuously forming the ring arround the invided nests tore away offspring carried by the inhabitants filled with panic.

As a result of the attack by *F. sanguinea* generally all experimentally established colonies of *F. exsecta* and *F. pressilabris* were completely destroyed. After the total extermination or dispersion of defenders and grabbing all larvae, pupae and even newly-hatched, colourless imaginal individuals *F. sanguinea* ants remain for some time in the area of the plundered nest. But gradually the number of new-coming individuals decreases and still greater numbers of individuals come back to their nest. With decreasing number of individuals along the trail, also the speed of their movements becomes lower. Separate *F. sanguinea* workers remain within the region of the battle for some hours after the withdrawal of main forces and they search the plundred nest. It may be suggested that these are the most sensitive individuals among *F. sanguinea* swarm.

It seems that *F. sanguinea* has specific signals to cease the attack when the situation becomes unfavourable to them. But the observations of this phenomenon can not be univocally interpreted because of the circumstances under which they were made.

It has already been noted that one of experimental *F. exsecta* nests was established outside the region searched by *F. sanguinea*, at a distance of about 15 m from their nests. This colony was not disturbed and survived to the next season, i.e., by the time when the range of the area searched by *F. sanguinea* was slightly extended. During the year of favourable existence the *F. exsecta* colony was well adapted to new habitat conditions, the nest was enlarged and gained a typical structure with the belowground part. Due to regular experimental introduction of new individuals, the *F. exsecta* society became very strong and it did not differ from natural colonies. In the summer of the next year after the establishment, even branches were periodically separated in this colony.

Due to the daily detailed observations of the experimental colony, the moment when the first *F. sanguinea* individual reached it was determined in mid-July. Since this time single *F. sanguinea* individuals approached the nest of *F. exsecta* more and more frequently during several successive days. They retired when *F. exsecta* individuals were on their way. As it could be expected, the location of the new nest by *F. sanguinea* was followed by a predatory expedition in a short time.

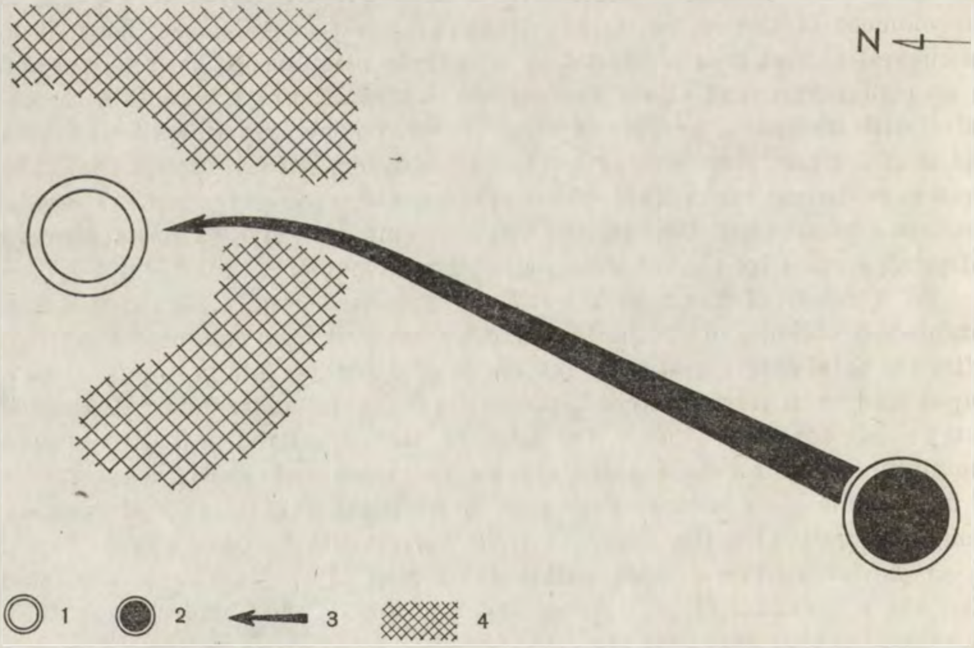


Fig. 4. Trail of the *F. sanguinea* raid on a *F. exsecta* nest: 1 – *F. exsecta* nest; 2 – *F. sanguinea* nest; 3 – trail of the raid; 4 – area covered with dense grass.

It should be noted that the trail of this raid was not rectilinear. The *F. exsecta* nest was bordered by a clump of thick, luxuriant grass from the side of the *F. sanguinea* nest. It was considerably thinned at one point, and the column of *F. sanguinea* moved rectilinearly from the nest just to this gorge, although it was not the shortest way, and then it turned towards the host nest (Fig. 4).

Therefore, the *F. exsecta* colony was threatened. But because of other observations started earlier this nest could not be destroyed nor could the nest of *F. sanguinea*. So, when it was evident that despite of successful defence of *F. exsecta* at the beginning, their colony can be exterminated, the nest of *F. sanguinea*, from which still greater number of aggressors arrived, was flooded to provoke the state of emergency there. But at least this measure was not followed by the expected response. That is why direct measures were applied to change the result of the battle. *F. sanguinea* individuals were moved from the foreground, where they dominated *F. exsecta*, to the interior of *F. exsecta* defence. After some time the situation in the battle-ground was reversed. *F. exsecta*, concentrated in large numbers at the base of the hill, surrounded the *F. sanguinea* individuals suddenly appearing among them. They immobilized them and carried into the nest.

The battle lasted 30 minutes more, and than the army of agressors was in retreat. The withdrawal, like the attack, was done by the majority of *F. sanguinea* individuals within a very short time. This indicates that the end of aggression under unfavourable circumstances is controlled by special signals recognized by these ants. Their nature is not known. It seems, however, that visual or tactile signals are of basic importance, as chemical signals are not likely to be so precise. It is also possible that the signal of withdrawal was not from the battle-ground but from the flooded *F. sanguinea* nest.

Independent of this, however, the recognition of retreat signals enlarge the list of so far known components of behaviour flexibility in these ants (Brun and Kutter 1949, Dobrzańska and Dobrzański 1960, Beck 1961, Czechowski 1975a). The flexibility of *F. sanguinea* ethology is usually opposed to the ritualistic behaviour of *P. rufescens* as these two species have similar mode of life. A fighting army of *P. rufescens* has no possibility of such communication. A case is known that a swarm of *P. rufescens* was exterminated when crossing the foraging trail of *Formica rufa* L. during successive raids, and also similar situations of this type were recorded (J. Dobrzański – personal communication).

2. Observations under natural conditions.

A raid of *F. sanguinea* on a polycalic colony of *F. cinerea* observed in the Kampinos Forest occurred in a specific situation and had a rather unusual pattern. A community including a number of nests was attacked and not a single nest as usually, which revealed some new features of *F. sanguinea* ethology. The colony, or rather the community of closely located *F. sanguinea* colonies, occupied a habitat characteristic of *F. cinerea*, i. e., a sandy, dry area covered with young trees predominated by birches and willows. The *F. cinerea* colonies were very numerous in this area. These ants were "slaves" in *F. sanguinea* colonies. The main sources of carbohydrate food for both *F. sanguinea* and *F. cinerea* were aggregations of aphids on birch shoots.

One of particularly abundant honeydew supply was used commonly by the two ant species. *F. cinerea* and *F. sanguinea* individuals searched without conflicts the common foraging ground. *F. sanguinea* workers passed near *F. cinerea* nests when going to the clump of trees infested with aphids, but it did not provoke any conflicts nor even anxiety in *F. cinerea*. Particular shoots of the infested trees were divided between the two species. A similar situation was observed when feeding traies with sugar were put in the area. Particular traies were used either one or by the other species, and although both the activity and the density of ants were increased, any serious conflicts were not observed. The encounting individuals of the two species sprang back suddenly, avoiding conflicts. Such situation was observed for about two weeks.

The behaviour of *F. sanguinea* was unexpectedly and suddenly changed n early July. On one day they searched the area in a different way since the

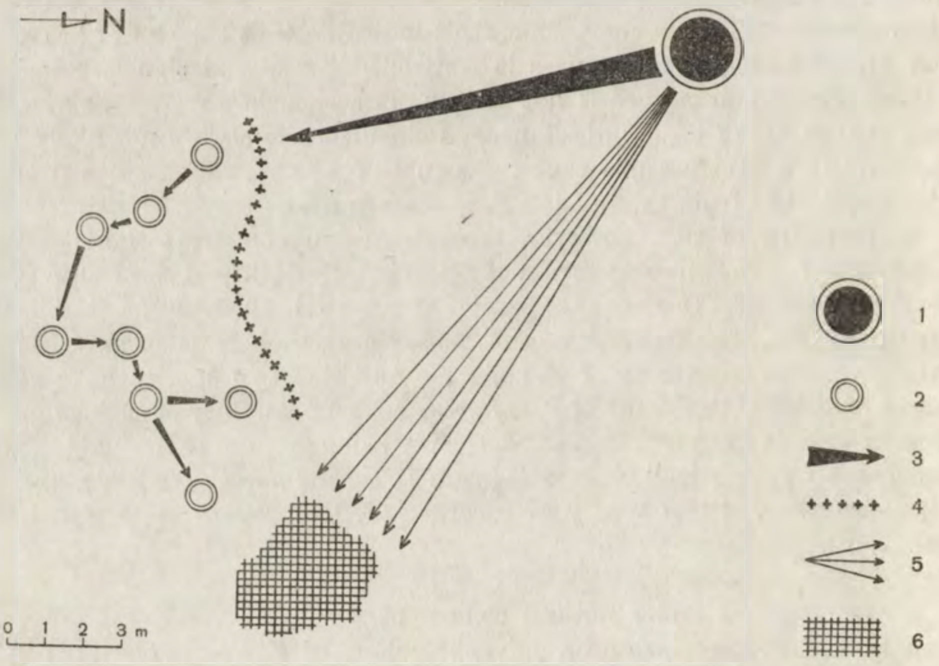


Fig. 5. Invasion of *F. sanguinea* on a polycalic colony of *F. cinerea*: 1 – *F. sanguinea* nest; 2 – *F. cinerea* nest; 3 – trail of the raid; 4 – line of the deposition of dead individuals by *F. sanguinea* workers; 5 – foraging trail of *F. sanguinea*; 6 – clump of birches infested with aphids used commonly as food by the two ant societies.

morning. *F. sanguinea* individuals approached the nests of *F. cinerea* first occasionally, then more frequently, and afterwards returned rapidly and in rush to their nest. A very characteristic and never observed behaviour was recorded: some ants carried dead individuals or their remains from the nest and deposited them at the border of the territory of *F. cinerea* (Fig. 5). The significance of this behaviour is not clear. Certainly, it was not a usual removing of dead ants from the nest, as in the place of deposition there was not the so--called "ant cemetery", nor similar facts were observed in the history of these two societies. The speed of movement of *F. sanguinea* individuals carrying dead bodies was considerably higher than during the performance of daily duties. It is possible that this behaviour can contribute to the onset of a raid, but it can be more simply explained.

In many ant species dead individuals are removed from the nest to "ant cemeteries". They are usually located at the border of the territory of a society, generally at the prolongation of foraging trails or near to them. Consequently, the individuals removing dead bodies tend to follow the beaten tracks. Due to the division of labour, dead bodies are removed by a special group of ants called "sextons" (Czechowski 1976). It may be expected that also in the *F. sanguinea* society there are similar rules. In the case described above the normal activity pattern of particular functional groups of ants was interrupted by the recruitment signal, which is the strongest stimulus of all. In this situation all individuals, including ,,sextons", abandoned their occupations and went in the direction imposed by the stimulus. Some conservatism characteristic of ants could account for the fact that "sextons" started the raid with dead bodies in their mandibles.

The next unexplained problem is the kind of stimulus responsible for the onset of aggression. The *F. sanguinea* society probably knew the attacked colonies of *F. cinerea* for a very long time. Therefore, the aggression could not be the result of signals announcing their location by individuals searching the area. It is possible that the density of the polycalic society of *F. cinerea*, which is a competitor, reached a threshold value under given habitat conditions, and it was the stimulus releasing aggressive behaviour in *F. sanguinea*. Another reason, perhaps more probable, could be an increase in carbohydrate food requirements of the *F. sanguinea* society, which could result either from an increase in the density or from the exhaustion of other energy resources. In this way interspecific competition could be intensified, and the disposition to fight characteristic of *F. sanguinea* was used to decide the ecological conflict.

Although the location of *F. cinerea* nest was known, the raid was organized in the same way as the raids on new-located nests. So, it can be supposed that the individuals starting it marked the way for the rest of the army either using trail pheromones or forming a "pheromone tunnel" of substances stimulating other ants. The course of the two-day battle was also interesting because not a single colony but the polycalic colony made up of more than ten nests was attacked. *F. sanguinea* individuals moved successively from one entrance of the *F. cinerea* nest to another, and the particular attacks on new objects situated tens centimeters from each other represented a kind of miniature raids. They recapitulated successive phases of a normal raid, with the only difference that not the nest of *F. sanguinea* was the starting point but the earlier invaded entrance to a nest of *F. cinerea*.

Detailed observations enables us to distinguish four basic phases in the battles around each attacked nest of *F. cinerea*:

1 — figths of single *F. sanguinea* individuals being the outpost of the main body of the army against also dispersed *F. cinerea* individuals approaching them (Fig. 6);

2 — fights of still single *F. sanguinea* individuals against already close ranks of *F. cinerea* (Fig. 7);

3 — ferocious battle of the main forces of the two species near the attacked nest (Fig. 8);

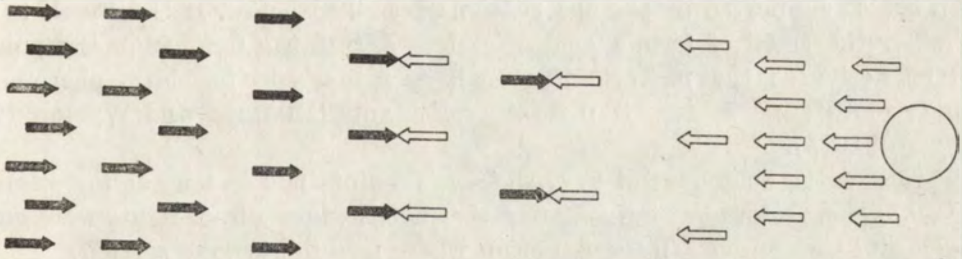
4 — the siege of the entrance to the nest (Fig. 9).

In phases 1 and 3 *F. sanguinea* individuals unquestionably predominate. Only in phase 2 the attacked ants predominate over the agressor. The phase of siege (4) begins when *F. cinerea* ants are dislodged from the foreground and shelter themselves in the nest. They form a ring inside the entrance hole to block it up. Occasionaly, an individual of any of the two species can catch an adversary. It is followed by the pulling of each other, and as the result either the *F. cinerea* individual is dragged out of the nest or the *F. sanguinea* individual is dragged into the host nest.

Particular phases of the conflict lasted from several to more than ten minutes, according to the size of the attacked nest and effectiveness of the defence. There were differences in the time of the siege of particular entrances. After some time each entrance was completely blocked from inside by the defenders, and the intruders raised the siege to attack the next colony.

Only in one case the state of siege lasted all the day and was finished with the end of the raid in the evening. This observation throws some light on the problem of alarm signals in *F. sanguinea*. The unusually prolonged siege of one of the *F. cinerea* nests was caused by its specific structure and location of the entrance in the bottom of a more than 10 cm-long, shallow fissure in the ground. The entrance was connected with a number of horizontal coridors spread radially under the ground. Due to the convenient configuration of the ground, the aggressors could readily reach the bottom of the fissure where they were captured by the defenders and tragged into side corridors. At the sime time, *F. cinerea* individuals going from the corridors to the bottom of the fissure were readily caught by the enemies waiting around above. As the result, direct fights between ants of the two species in this place were continued for many hours.

This observation indicate that the substance stimulating other individuals is most intensively excreted by *F. sanguinea* during direct fights. This conclu-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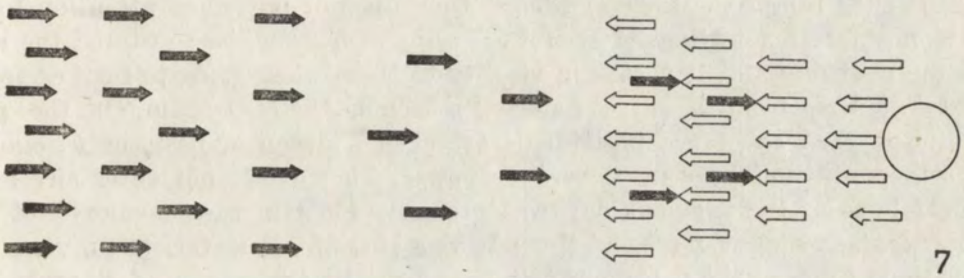
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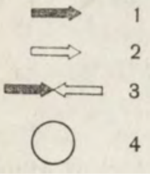


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Figs 6–9. Successive stages of the battle between *F. sanguinea* and *F. cinerea*: 1 — an individual of *F. sanguinea*; 2 — an individual of *F. cinerea*; 3 — fight; 4 — entrance to *F. cinerea* nest. (Description in the text).

sion is also supported by the observations described below. It is difficult to tell whether the smell of formic acid excreted during the fight from the poison--gland activates the nearest individuals or rather specific alarm pheromones which were found in American *Raptiformica* ants (Regnier and Wilson 1971, Wilson 1975).

Aggressive behaviour of *F. sanguinea* is maintained as long as the stimulus acts. The aggressors left immediately the places where direct fights were continued, and they moved in the direction where new fights were started.

Further observations indicated that the aggressiveness of *F. sanguinea* workers was stimulated by both the capture of a representative of their own species by *F. cinerea* and the capture of *F. cinerea* by them.

If they raised the siege of a nest, they did not pay more attention to it. Such nests were not attacked even if the army of *F. sanguinea* restored the raid on the next day and it passed in vicinity to them when going to further nests, and *F. cinerea* from these nests started searching the area again. On the preceding day *F. sanguinea* individuals attacked a dozen of nests of *F. cinerea* but they did not grab any larvae or pupae. They could not enter any nest. The failure of the previous day was probably fixed in the "memory" of the *F. sanguinea* society for some time. It was possible, however, to provoke the invasion of any of the nests indifferently passed by the column of *F. sanguinea* and also to prolonge the siege at will if single invaders were introduced into the entrance hole. It confirms the conclusion that alarm signals are used during the fight, and at the same time, it rids of the possible objection that kinopsis, i. e. optical stimulation by violent movements is of basic importance and not a volatile alarm substance. In most cases individuals introduced into the entrance and violently fighting under the ground were not visible from the outside, but all *F. sanguinea* which were in vicinity to this nest responded to the fight. At first, individuals present within a distance of dozen centimeters approached the nest, which was followed by a chain reaction involving more distant ants. This indicates that the stimulus of fight is transferred to the next individuals by those which were stimulated earlier. The signals described above ensure to *F. sanguinea* the mutual help in danger. But this response can be fully developed only when ants already reached a certain level of stimulation.

As it has already been noted, the described raid did not provide the *F. sanguinea* society with any booty, but from the ecological point of view it was successful as *F. cinerea* foragers were dislodged from the clump of birches where the two species foraged jointly before the battle.

Recruitment and raids in *Polyergus rufescens*

The way of the location of nests of slave species by *P. rufescens* and direction of the raids are still problems under discussion. They were analysed earlier (Czechowski 1975b).

Raids are always started by the same group of several dozen individuals, markedly different from other ones, no matter if and in which way the location of an appropriate host nest is signalized. These are the so-called "activators" — a functional group made up either of most sensitive individuals (DOBRZAŃSKA and DOBRZAŃSKI 1960) or of those with better developed glands of external secretions (pheromones) (CZECHOWSKI 1975b). In any case the "activators" have the highest activity level of all the other individuals.

The frequency distribution of the activity of particular individuals in the *P. rufescens* society is discontinuous. From this point of view, the "activators" form a separate group. Frequency distribution of their activity is separated by a considerable interval from that of the other individuals (Fig. 10). At the other tail of frequency distribution there are "stragglers", the most delayed individuals. But the "stragglers" are not a clearly separated group. The decrease in individual activity is continuous and gently goes from the values characteristic of the members of the main forces to those of the "stragglers".

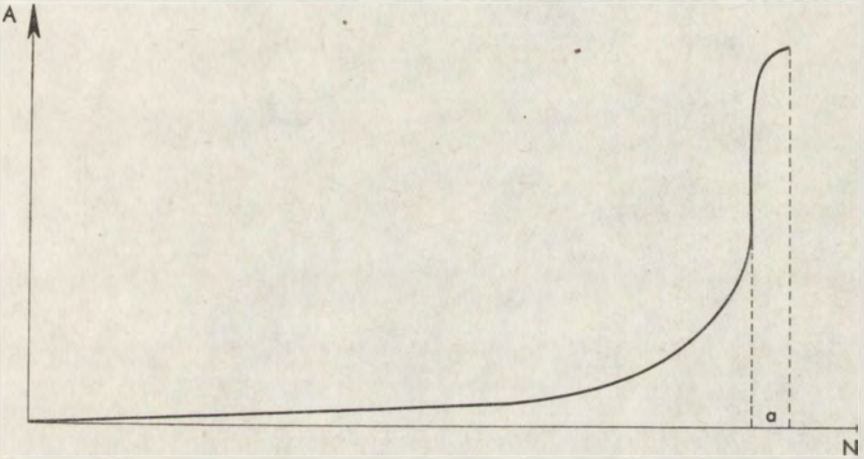
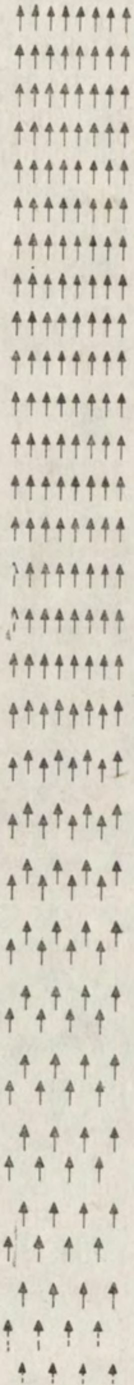


Fig. 10. Activity distribution of particular individuals within a *P. rufescens* swarm: 1 — degree of activity; N — numbers; a — group of the "activators".

Before the raid is started, the "activators" go out on the surface. They form a cluster circulating around the nest, and involving still more individuals. The movements of ants are firstly chaotic, nonorganized, but gradually they become still more ordered. The circle of the "activators" stretches out in the direction in which the predatory expedition is continued subsequently.

Unlike *F. sanguinea*, *P. rufescens* start their raids in a dense mass with conspicuously marked head of the column, and all individuals walk in the same direction (Figs. 11 and 12).

The mobilization of the column and its direction depend directly on the primary movement of the "activators". If these ants removed from the swarm,



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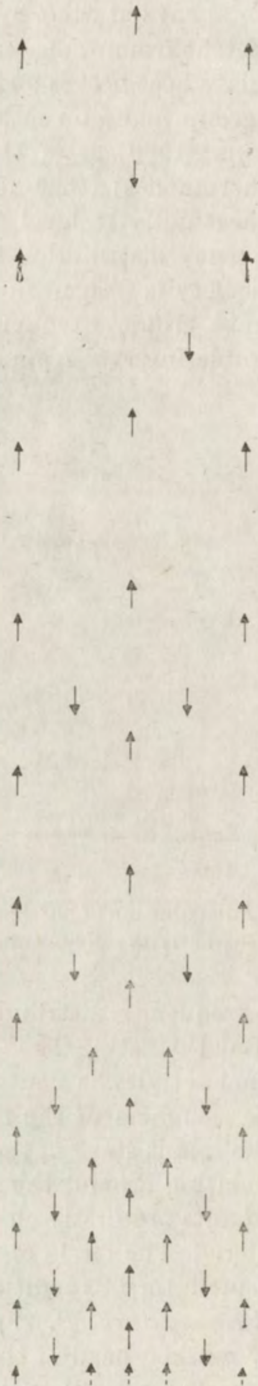

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Figs 11–12. **Scheme of a marching column of *P. rufescens* (11) and *F. sanguinea* (12).**

the raids are not more organized. Experimental replacement of the majority of "activators" in another direction than that primarily established is followed by the raid in this new direction (Dobrzańska and Dobrzański 1960).

These observations seem to show that the role of the "activators" lies in stimulating the whole society by means of pheromones, and the army follows the direction indicated by the highest concentration of alarm substance. But the final evidence can only be provided by appropriate experiments with substances extracted from the bodies of *P. rufescens* workers.

The moment of almost instantaneous mobilization of the whole *P. rufescens* army is similar to the mass attack of *F. sanguinea* on a host nest. The impression is that these two phenomena can have a common mechanism. Therefore, it may be suggested that the mobilization of the *P. rufescens* column coincides with a treshold of the concentration of recruitment pheromone laid down by the "activators" and individuals joining them in increasing numbers.

Changes in the composition of the head of the column are characteristic of *P. rufescens* raids. Ants in the head of the column walk a dozen to several dozen centimeters and then they rapidly turn aside, almost stop, and join the main body of the column leaving them behind. It may be suggested that such behaviour can be the effect of the fact that ants in the head of the column lay down a volatile substance tracing the way and stimulating ants behind.

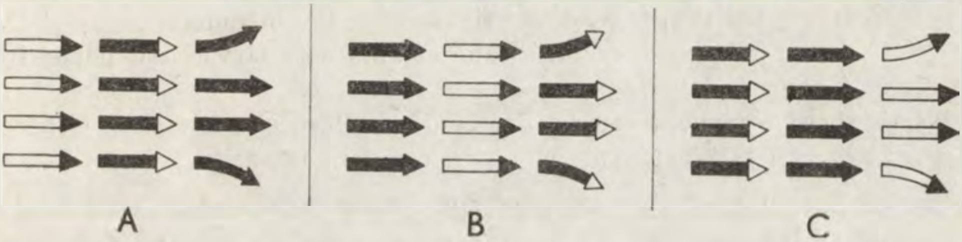


Fig. 13. Changes in the composition of the head of a *P. rufescens* column: A, B and C — successive phases of the movement of ants.

It is possible that the ants passing to more distant ranks exhausted the whole pheromone resources and they retire to follow the attractive secretion laid down by their successors. The movements of individuals temporarily forming the head are similar to the movements of the "activators" initiating the raid. In this way the stimulus forcing ants to continue the raid could permanently be ahead, which enables the ants to maintain still the same direction. The trail of *P. rufescens* is always strictly rectilinear.

Approaching a nest of the slave species, the head of the *P. rufescens* column stops and the ants stretching for several metres concentrate now and scatter afterwards through an area of several square metres in search of entrances to the nests. When the first individuals find an entrance to the foreign nest, the rest of the intruders searching the area form at once a column going there. A rapid and common onset of this response indicates that it is effected by a stimulus dispatched at a very high rate, thus, by chemical or acoustical signals. Optical signals (kinopsis) must be excluded as all ants are involved, even those hidden from sight.

Unlike in *F. sanguinea*, in *P. rufescens* there is no mutual help in danger. If the column passes in vicinity to a foreign nest plundered the previous day or not attacked for other reasons, it frequently happens that single *P. rufescens* are captured and killed by inhabitants of this nest. Although there are violent flights in such cases, the main forces continue the way without any response. Nor there is any response in the case when particular individuals caught and immobilized by some workers defending the nest during the invasion, made desperate attempts to liberate themselves. In similar situations *F. sanguinea* ants try to help immediately such individuals.

Alarm signals in ants attacked by *Formica sanguinea* and *Polyergus rufescens*

The behaviour of ants attacked by *F. sanguinea* or *P. rufescens* armies was observed during each predatory expeditions. The response of *Formica exsecta*, *F. pressilabris*, *F. pratensis* and *F. cinerea* to the raid of *F. sanguinea* was studied, and also the response of *F. cinerea* and *F. fusca* attacked by *P. rufescens*.

In general, two types of defence can be distinguished:

– an active defence, i. e., direct fights with the intruders;

– a passive defence, i. e., an escape of ants with larvae and pupae from the zone of danger.

Both these responces can be detected in all species attacked either by *F. sanguinea* or by *P. rufescens*, but with different intensity.

1. The responce of ants attacked by *Formica sanguinea*.

It has been found that the pheromones excreted by fighting *F. pergandei* and *F. subintegra*, North American species of the subgenus *Raptiformica*, which are related to *F. sanguinea*, have an inactivating effect on defenders of the attacked colony of *F. subsericea* (Regnier and Wilson 1971, Wilson 1975). In the case of a *F. sanguinea* attack, the defence of the nests of all the species quoted above is continued till the end of the conflict. There is no indication, hovewer, of chemical "propaganda".

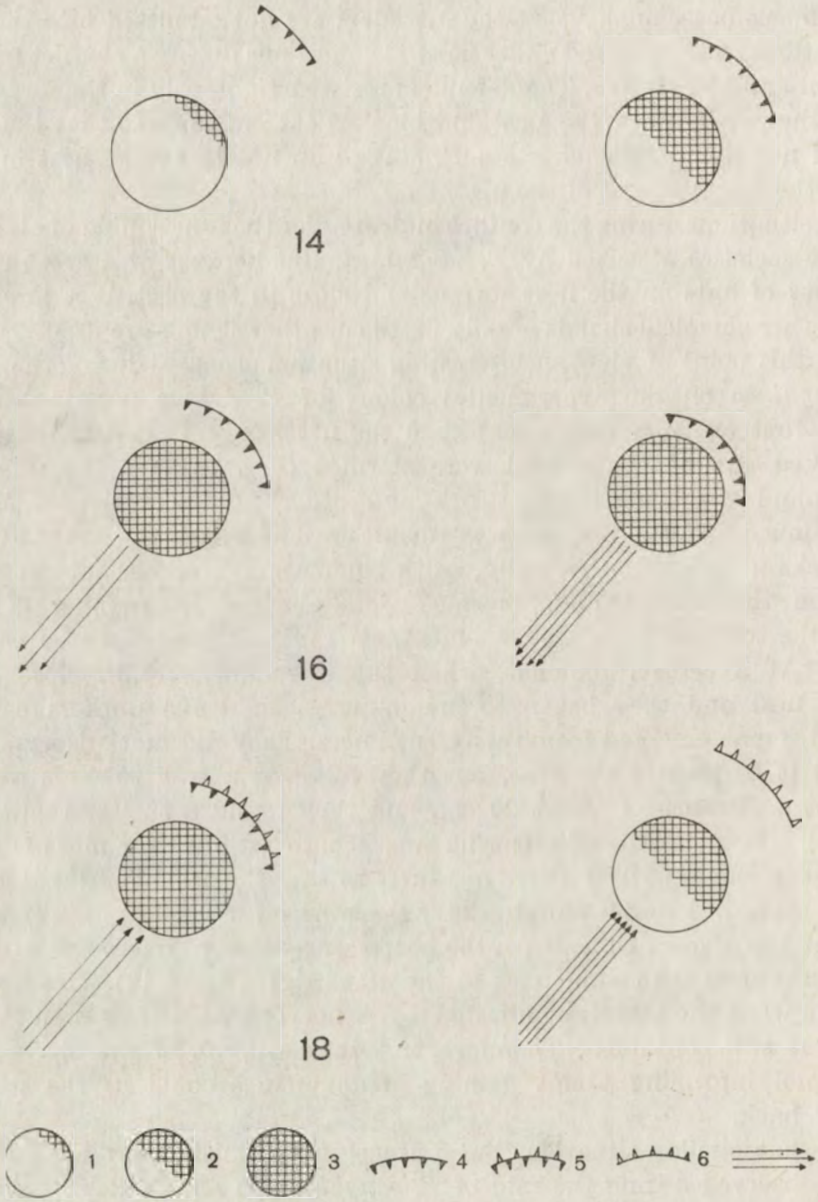
When the intruders enter the nest, a part of host workers carry larvae and pupae onto the surface. The ants saving the offspring try to cross the zone occupied by *F. sanguinea* and, if they are successful, they do not leave the larvae and pupae but they wait in shelter till the end of the invasion, sometimes for several hours. To protect themselves, they frequently use long stems of grasses growing around the border of the nest. The remaining individuals persistently fight till they are killed. It should be noted, however, that the attack of *F. sanguinea* on *F. fusca* colonies was not observed. The workers of this species are most frequently "slaves" in societies of European ants which are social parasites, and it is possible that during such conflicts the effects of chemical "propagation" can be observed.

It happens occasionally that the intruders are not admitted into the nest. Such situations were observed under natural conditions during a conflict between *F. sanguinea* and *F. cinerea*. The defenders resisted vigorously in the foreground and then they retiredinto the nest and blocked the entrance so that the intruders could not enter. In such cases *F. cinerea* do not leave the nest in panic nor carry the offspring out of the nest.

Some situations during the conflict indicated for the functioning of alarm signals in the societies attacked by *F. sanguinea*. But because of a great density and activity of ants on the nest surface and close to the nest, it is impossible to tell whether chemical signals or only tactile or other signals are used.

From this point of view an interesting situation occurred during the attack of *F. sanguinea* on the experimental colony of *F. exsecta* described above. When the first few intruders approached the nest, only *F. exsecta* present on the attacked site of the mound were alarmed (Fig. 14). On the other site of the mound the construction work and other normal activities of ants were continued. This situation was maintained for some time after the first attacks (Fig. 15). Gradually, with increasing number of intruders, all ants on the whole mound surface were alarmed. A number of them came to the surface from inside and they ran touching themselves with antennae. At a certain moment, when the intruders were in close vicinity to the nest and they began to predominate, suddenly workers carrying larvae and pupae emerged from many entrances. They did not disperse, however, as it is frequently the case, but they followed a trail towards a clump of grass at a distance of about 20 cm, and they found a shelter there (Figs. 16 and 17). The removing of offspring was being continued for more than ten minutes when the described above measures to save the nest against extermination were applied. A dozen minutes later the workers with pupae did not leave the nest, and in a short time, when the battle was still continued, the ants sheltered in grass started to come back to the nest (Figs. 18 and 19). This happend at the time when the alarm, manifested by a nervous walk of ants on the nest surface, was still continued. Therefore, not the cessation of the alarm but a special signal informing about gaining predominance could be the stimulus to coming back.

Somewhat similar situation, but unsuccesfully finished for the attacked ants, was observed during the raid of *F. sanguinea* on an artificial colony of *F. pratensis*. This relatively large colony was established between a nest of *F. sanguinea* and an area occupied by some small branches of *F. exsecta* and *F. pressilabris* used for the studies of another kind. It was expected that this nest formed a natural obstacle to *F. sanguinea* on their way towards the experimental colonies. It was expected that *F. pratensis* would be able to resist successfully a possible attack as they were strong and numerous.



Figs 14–19. Successive phases of the battle between *F. sanguinea* and *F. exsecta*: 1, 2 and 3 – extending alarm response of ants on the surface of the ant-hill; 4 – line of fights – *F. sanguinea* predominate; 5 – line of fights – turning-point in the battle; 6 – line of fights – *F. exsecta* predominate; 7 – movement of *F. exsecta* workers carrying pupae. (Description in the text).

The raid of *F. sanguinea* on this colony was started the next day after its establishment. At the beginning, *F. pratensis* predominated and they killed large numbers of approaching intruders. But about an hour later they began to retreat, *F. sanguinea* becoming still more abundant. As soon as the intruders gained predominance, *F. pratensis* individuals started to escape with the offspring from the threatened nest. A dense group of them, made up about 1000 individuals, passed several meters in an open space, then they turned in the direction of the nest, passed it round (it was totally invaded by *F. sanguinea*) and walked down a steep slope densely covered with the vegetation where they could not be observed longer (Fig. 20). But the area of the battle was left only by the individuals with offspring. The other individuals resisted till the end.

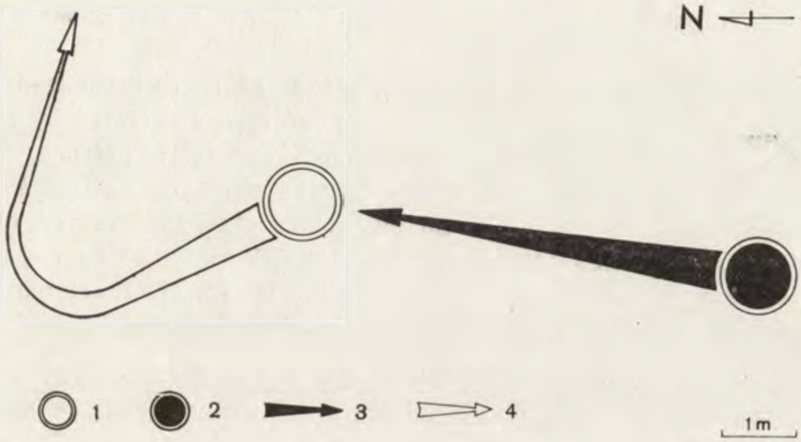


Fig. 20. Invasion of *F. sanguinea* on an experimental colony of *F. pratensis*: 1 – *F. pratensis* nest; 2 – *F. sanguinea* nest; 3 – trail of the raid; 4 – trail of the escape of *F. pratensis* workers with the offspring.

It can be suggested, however, than if the experimental branch of *F. pratensis* colony had had enough time to reach a certain stabilization, the *F. sanguinea* army would not probably have been succesful.

2. The response of ants attacked by *Polyergus rufescens*.

Unlike in the case of *F. sanguinea* attacks, the active defense of colonies attacked by *P. rufescens* is very short and limited to the first phase of the conflict. *F. cinerea* or *F. fusca* attack exclusively the first *P. rufescens* individuals which approach singly to their nests. When the whole army of intruders go inside the nest through the entrances, the attacked ants do not fight. Few of them run in all directions among *P. rufescens* individuals on the surface of the nest. Some of them try to raise barricades in entrances, using small stones, sticks, etc., but they are not effective. One *P. rufescens* individual can destroy such barricades at once. The intruders search for offspring in the invaded nest for 1–2 minutes, and then, first singly, later still in greater masses, appear on the nest surface with larvae and pupae. They are followed by host ants trying to restore their offspring. All of them disperse in the area. The larvae and pupae removed from the nest and sheltered in its vicinity are saved because *P. rufescens*, unlike *F. sanguinea*, are interested only in the offspring found inside the nest. Due to remarkably developed rituals of behaviour they do not respond to larvae and pupae found outside the nest.

Two reasons may be found to explain almost complete lack of defence response in ants attacked by *P. rufescens*:

– surprise caused by a sudden invasion of several thousand enemies;

– effect of specific "psychogases" or pheromones excreted by *P. rufescens* which have a destructive effect on the possibility of active defence.

Chemical "propaganda" of this kind was observed during *F. pergandei* and *F. subintegra* raids, still a certain active defence occurred in attacked ants *F. subsericea* (Regnier and Wilson 1971, Wilson 1975). So, if a similar mechanism is involved during *P. rufescens* raids, it seems be much more effective.

Summary

1. Organization of predatory expedition of "slave-making" ants such as *F. sanguinea* and *P. rufescens* is based on a precise communication system in which pheromones are of basic importance.

2. Chemical signals play an important role in all phases of the raid from mobilization, through the battle, to retreat with booty.

3. Unlike *P. rufescens*, *F. sanguinea* ants have a specific retreat signal due to which they can avoid excessive losses when they are predominated by the attacked ants.

4. In *F. sanguinea* there is a mutual help in danger, controlled by chemical signals, which is not observed in *P. rufescens*.

5. Inherited tendency to fight in *F. sanguinea* is also used to decide ecological conflicts with ants of other species.

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STRESZCZENIE

[Tytuł: Sygnalizacja rekrutacyjna i przebieg rajdów u mrówek organizujących wyprawy rabunkowe]

Wyprawy rabunkowe po obce potomstwo, jakie mrówki *Formica* (*Raptiformica*) *sanguinea* Latr. i *Polyergus rufescens* Latr. urządzają do mrowisk innych gatunków, odbywać się mogą, jako akcje wymagające współdziałania wielkiej liczby osobników, dzięki istnieniu precyzyjnego systemu zawiadamiania i wymiany informacji między poszczególnymi członkami społeczeństwa. Prawdopodobnie najważniejszą rolę odgrywa tu sygnalizacja chemiczna – feromonowa.

1. Rekrutacja i przebieg wypraw u *F. sanguinea*.

Badania przeprowadzono przy użyciu eksperymentalnie zakładanych mrowisk (*Formica exsecta* Nyl., *F. pressilabris* Nyl. i *F. pratensis* Retz.) w pobliżu gniazda *F. sanguinea* oraz obserwując w warunkach naturalnych przebieg agresji *F. sanguinea* na polikaliczną kolonię *Formica cinerea* Mayr. Stwierdzono, że osobnik *F. sanguinea* po napotkaniu odpowiedniego do napaści obiektu zawiadamia o tym swoje społeczeństwo, co powoduje natychmiastowe rozpoczęcie akcji bojowej. Kolumna marszowa *F. sanguinea* jest luźna i pozbawiona wyraźnej czołówki – poszczególne osobniki włączają się do akcji sukcesywnie i zagęszczenie napastników na trasie pochodu wzrasta stopniowo, pod koniec zaś wyprawy stopniowo maleje. Charakterystyczny dla kolumny *F. sanguinea* jest ruch dwustronny. Rola mrówek biegających w obydwu kierunkach trasą wyprawy i nie angażujących się w walkę ani rabowanie potomstwa z napadniętego mrowiska polega, jak się wydaje, na feromonowym oddziaływaniu na resztę armii. Możliwe są następujące sposoby interpretacji tego zjawiska: 1 — mrówki biegające w obu kierunkach wytwarzają wzdłuż trasy wyprawy „tunel feromonowy" pozwalający na utrzymanie właściwego kierunku marszu kolumny; 2 — osobniki zawracające od obiektu ataku do swego gniazda pobudzają do wymarszu pozostające tam jeszcze robotnice; 3 — mrówki te odnawiają być może ślad zapachowy pozostawiony przez osobniki, które pierwsze odnalazły obce gniazdo.

Mrówki *F. sanguinea* dysponują odpowiednim systemem sygnalizacji, umożliwiającym wycofanie się armii w przypadku nawiązania walki z przeważającymi siłami przeciwnika. Stwierdzono także, że u tego gatunku występuje zjawisko wzajemnej pomocy udzielanej zagrożonym osobnikom przez mrówki znajdujące się w pobliżu, a reakcję tę wywołują sygnały chemiczne.

Wrodzona mrówkom *F. sanguinea* skłonność do walki wykorzystywana bywa nie tylko do zdobywania „niewolników", lecz także ma znaczenie ekologiczne, zapewniając społeczeństwom tego gatunku przewagę w sytuacjach konkurowania o pokarm z innymi mrówkami. W takim przypadku obce mrowiska mogą być przez długi czas znane i nie niepokojone przez społeczeństwo *F. sanguinea*. Dopiero zaostrzenie się konkurencji pokarmowej wywołane określonymi czynnikami zewnętrznymi lub wewnątrzrojowymi doprowadza do konfliktu — napaści roju *F. sanguinea* na społeczeństwo konkurujące (w obserwowanym przypadku — *F. cinerea*).

2. Rekrutacja i przebieg wypraw u *P. rufescens*.

Wymarsz kolumny *P. rufescens* wywołany jest zachowaniem się funkcjonalnej grupy robotnic wyodrębnionej z reszty roju — tzw. „aktywistów". Mrówki te krążąc wokół swego gniazda tworzą ruchliwe skupisko, do którego włączają się inne osobniki. Następnie kierunek ich ruchu ustala się i wyznacza kierunek inicjowanego rajdu (Dobrzańska i Dobrzański 1960). Można sądzić, że rolą aktywistów jest feromonowe pobudzanie reszty społeczeństwa.

Kolumna *P. rufescens* jest zwarta, a czoło pochodu wyraźne. Charakterystyczna jest tu płynność czołówki — do przodu wysuwają się coraz to inne mrówki, zastępując poprzednich przewodników. Być może, mrówki z pierwszych szeregów wydzielają odpowiedni feromon, a po wyczerpaniu się jego zapasu odchodzą do tyłu. Dzięki temu bodziec do postępowania naprzód znajduje się stale na czele kolumny i pozwala utrzymać prostoliniową trasę pochodu. Po dojściu w pobliże obcego gniazda mrówki rozpraszają się w poszukiwaniu otworów wejściowych, a osobnik, który pierwszy je odnajduje, sygnalizuje to feromonowo (?) pozostałym.

3. Reakcje mrówek napadniętych przez *F. sanguinea* i *P. rufescens*.

Mrówki napadnięte przez armię pasożyta społecznego podejmują dwa rodzaje obrony: czynną, tzn. walkę bezpośrednią oraz bierną — ucieczkę z potomstwem poza strefę zagrożenia. W czasie napadów *P. rufescens* na mrowiska

F. cinerea czy *F. fusca* czynna obrona prawie nie występuje. Możliwe, że jest to spowodowane demobilizującym na obrońców działaniem feromonów wydzielanych przez osobniki *P. rufescens*, podobnie jak stwierdzono to w przypadku rajdów północnoamerykańskich gatunków mrówek z podrodzaju *Raptiformica* (Regnier i Wilson 1971).

РЕЗЮМЕ

[Заглавие: Мобилизационная сигнализация и ход нападения у муравьев, организующих набеги на колонии других муравьев]

Грабительские набеги за потомством иных видов муравьев, совершаемые муравьями *Formica* (*Raptiformica*) *sanguinea* Latr. и *Polyergus rufescens* Latr., будучи мероприятиями, требующими взаимодействия большого количества особей, могут иметь успех благодаря существованию точной системы сообщения и обмена информациями между отдельными членами сообщества. По-видимому, основную роль играет тут химическая сигнализация — феромоновая.

1. Мобилизация и ход набегов у *F. sanguinea*.

Исследования произведены при помощи созданных экспериментально муравейников *Formica exsecta* Nyl., *F. pressilabris* Nyl. и *F. pratensis* Retz. поблизости гнезда F. *sanguinea*, а также путем наблюдения в естественных уловиях за ходом нападения *F. sanguinea* на поликалическую колонию *Formica cinerea* Mayr. Констатировано, что особь *F. sanguinea*, встретивь соответствующий для нападения объект, извещает об этом свое сообщество, и боевая операция начинается немедленно. У *F. sanguinea* походная колонна разрознена и лишена четкой головной группы — отдельные особи включаются последовательно, и плотность колонны по дороге постепенно возрастает, а под конец похода постепенно уменьшается. Для колонны *F. sanguinea* характерно двустороннее движение. Роль муравьев, бегающих в обоих направлениях трассы похода и не принимающих участие ни в борьбе, ни в грабеже потомства из колонии, на которую нападают, заключается, как кажется, в феромоновом воздействии на остальную „армию". Это явление можно было бы интерпретировать следующим образом: 1 — муравьи бегающие в обоих направлениях создают вдоль трассы похода „феромоновый туннель", благодаря которому поддерживается надлежащее направление движения колонны; 2 — особи, которые возвращаются обратно к гнезду, побуждают к выступлению находящихся еще там рабочих муравьев; 3 — может быть, муравьи восстанавливают следы запаха, оставленные особями, которые первые обнаружили гнездо другого вида.

Муравьи из вида *F. sanguinea* имеют соответственную систему сигнализации, дающую возможность отступить нападающей армии в случае, если противник оказался сильнее. Констатировано также, что у этого вида имеет место явление взаимопомощи, оказываемой особям находящимся в опасности, муравьями, нахо-

дящимися поблизости, а такая реакция вызывается при помощи химической сигнализации.

Врожденная склонность к борьбе у *F. sanguinea* используется не только для овладения ,,рабами'', она имеет также экологическое значение, обеспечивая сообществам этого вида перевес в межвидовой конкуренции за пищу. Чужие муравейники могут длительное время находится вблизи сообщества *F. sanguinea* и не подвергаться беспокойству; и лишь обострение пищевой конкуренции, вызванное внешними или внутренними факторами, приводит к конфликту — нападению роя *F. sanguinea* на конкурентное сообщество (как это наблюдали в случае *F. cinerea*).

2. Мобилизация и ход набегов у *P. rufescens*.

Выступление колонны *P. rufescens* побуждает поведение так наз. ,,активистов'' — функциональной группы рабочих муравьев, выделенных из роя. Эти муравьи, описывая круги вокруг своего гнезда, создают подвижную группу, к которой присоединяются другие особи. Затем устанавливается направление движения планируемого похода (Dobrzańska и Dobrzański 1960). Можно предположить, что роль активистов заключается в феромоновом возбуждении остальных особей.

Колонна у *P. rufescens* сплоченная, с четко выраженной головной группой. Но характерно непостоянство головной группы — происходит постоянный обмен особей, вперед выдвигаются новые муравьи, заменяя предыдущих проводников. Может быть, муравьи из первых рядов выделяют соответственный феромон, а когда его запас исчерпается, они отходят назад. Благодаря этому раздражитель, побуждающий к движению вперед, всегда находится в голове колонны и позволяет удерживать прямолинейную трассу похода. Подойдя ближе к чужому гнезду, муравьи рассеиваются в поисках входов в гнездо. Особь, которая первая его найдет, сигнализирует это феромоново (?) остальным.

3. Реакции муравьев, подвергшихся нападению со стороны *F. sanguinea* и *P. rufescens*.

Муравьи, на которых напала армия общественного паразита, обороняются двояким образом: активно, то-есть путем непосредственной борьбы, или пассивно, обращаясь в бегство вместе с потомством из опасной зоны. Во время нападения *P. rufescens* на муравейники *F. cinerea* или *F. fusca* активной обороны почти не наблюдается. Возможно, что это вызвано демобилизирующим воздействием феромонов, выделяемых особями *P. rufescens*, на обороняющихся муравьев, как это констатировано в случае походов североамериканских видов муравьев из подрода *Raptiformica* (Regnier and Wilson 1971).

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