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Wojciech CZECHOWSKI

Functioning of a mixed colony of *Formica sanguinea* LATR. + *F. polyctena* FOERST. (*Hymenoptera*, *Formicidae*) with a surplus of slaves

[With 6 tables and 5 figures in the text]

Abstract. About 230,000 pupae of *Formica polyctena* FOERST. workers were introduced into a monocalic colony of *F. sanguinea* Latr. The result was a mixed colony consisting up to 96% of slaves of the non-typical species. The reactions of *F. sanguinea* to this situation, the development of the mixed colony, division of labour within the colony and relations with a nearby (artificially founded) colony of *F. polyctena* were investigated. The experiment was carried out in Gorce (the Western Beskidy Mts.) in 1987.

INTRODUCTION

Formica (*Raptiformica*) *sanguinea* LATR. is a common Palaearctic species which occasionally practises slavery. The typical slaves of these ants are workers of species of the subgenus *Serviformica* FOR., most frequently *Formica fusca* L. Only exceptionally have *F. sanguinea* slaves of other subgenera of the genus *Formica* L.: *Coptoformica* MÜLL. (*F. exsecta* NYL., *F. pressilabris* NYL.) and *Formica* s. str. L. (*F. truncorum* FABR., *F. pratensis* RETZ., *F. rufa* L., *F. polyctena*) (STITZ 1914, MARIKOVSKY 1963, CZECHOWSKI 1975, 1977, MABELIS, personal communication). It is very easy to initiate artificially a non-typical mixed colony by supplying *F. sanguinea* with alien pupae or by establishing in the neighbourhood an "artificial" nest of any species of the subgenus *Coptoformica* or *Formica* s. str. Immediately, such a nest is completely plundered, and the stolen pupae emerge as non-specific slaves. In the course of artificial colonization of red wood ants, it is necessary to pay attention to any likely presence of *F. sanguinea* in the vicinity because of the enormous aggressiveness of the latter (MARIKOVSKY 1963).

The present paper is a result of investigations connected with artificial colonization of *F. polyctena* in the Gorczański National Park, carried out by the Institute of Zoology PAS (Czechowski 1989). The investigations were undertaken in order to study the behaviour of *F. sanguinea* ants when the availability of pupae of a non-typical slave species (*F. polyctena*) was practically boundless and to record the development of a mixed colony formed under such conditions, the division of labour within the nest, the evolution of mutual relations between the mixed colony of *F. sanguinea* and *F. polyctena*, where the slaves greatly outnumbered the hosts, and an ordinary colony of *F. polyctena*.

Up till now, information on the above questions has been scanty and usually of general nature. As far as division of labour within a mixed colony of slave-maker ants is concerned it is known that, as a rule, slaves carry out tasks within the nest (care of the offspring) (Wheeler 1910, Dlussky 1967, Marikovsky 1967) and any participation in outside, tasks depends on their abundance in relation to that of the swarm of the hosts. The more slaves, the greater their share in such tasks as foraging or nest building (Marikovsky 1963). According to Sakagami and Hayashida (1962) the percentage of slaves (*F. japonica* Motsch.) among builders can be even higher than that of *F. sanguinea* – the higher this number, the greater is the abundance of a given mixed colony. Unfortunately, the above-mentioned papers provide few concrete quantitative data. Very interesting is Marikovsky's report (1963) about cases of autonomization of swarms of non-typical slaves (*F. rufa*) when they greatly outnumber *F. sanguinea*. The essence of this phenomenon remains unknown.

STUDY AREA

Gorce are a small mountain range in the Western Beskidy (the Western Carpathians). *F. sanguinea* is a moderately frequent species there; under natural conditions *F. fusca* and *F. lemani* Bondr. are its slaves. The investigations were carried out in the valley of the stream Jaszcze at 840 m above sea level, near the village Ochotnica Górna, in 1987. The site of the experiment was situated in a grass belt, from several to over a dozen metres wide, between a road and the edge of a beech-spruce-fir forest (Fig. 1). In this ecotone with a southern exposure the natural myrmecofauna consisted of the following species: *F. sanguinea* – a primary dominant in the competition hierarchy of the community [in accordance with the concept of Pisarski and Vepsäläinen (1984, 1988), and Savolainen and Vepsäläinen (1988)], *Myrmica ruginodis* Nyl. – the most frequent species, and *Leptothorax* sp., *Tetramorium caespitum* (L.), *Lasius niger* (L.), and *Formica fusca*. The density of nests was very high at some places; at stony ones it reached 4 per 10 m^2. *F. polyctena* was an additional element, introduced artificially into that habitat, and during the studies it was the actual dominant in the hierarchy of the community.

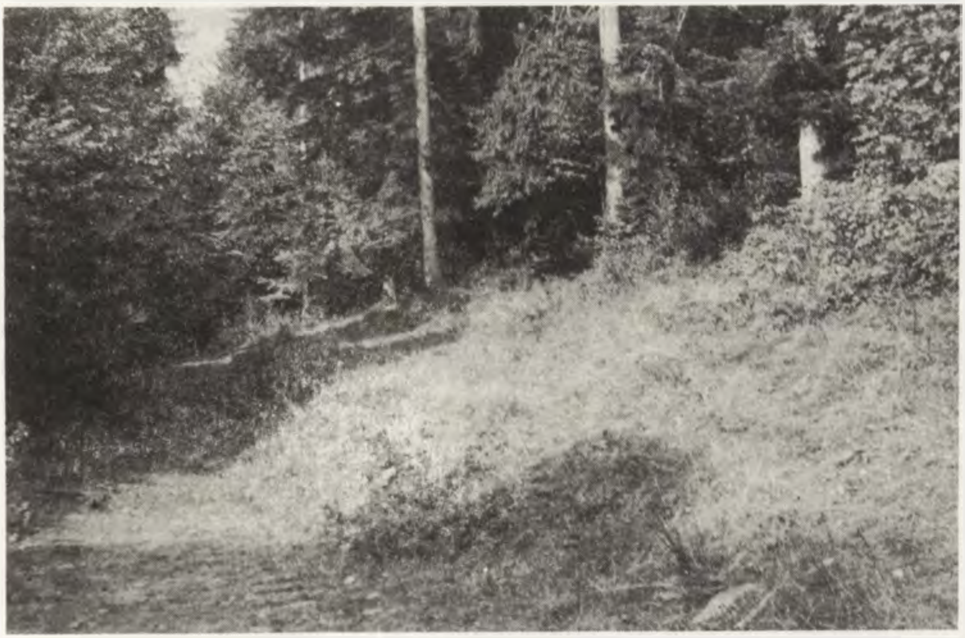

Fig. 1. Study area (photo by W. Czechowski).

OBJECTS OF THE STUDY

Formica sanguinea. In 1986, i.e. in a year before the study began the society of this species formed a polycalic colony of several nests. In July 1986, an artificial colony of *F. polyctena* was established at a distance of 15 m from the nearest nest of *F. sanguinea*. A conflict between these two species, at the beginning very dramatic for *F. sanguinea*, brought about a recession and territorial shift of the society of *F. sanguinea*. In the spring of 1987, just before the beginning of the experimental work, this society inhabited only one nest, about 3 m from places where very soon (in June) border stations of the colony of *F. polyctena* sprang up spontaneously. When this happened, *F. sanguinea* moved nearly 10 m beyond the penetration zone of *F. polyctena*. There it built a new nest. At the time when the experiment started (the beginning of July) the dimensions of the mound were: $\varnothing = 15/20$ cm, $h = 5$ cm. At a distance of 4 m, in a cluster of blackberry bushes, on the edge of the forest there was a deserted (winter?) nest of *F. sanguinea* and it had the following dimensions: $\varnothing = 30$ cm, $h = 10$ cm. An inhabited nest of *F. sanguinea* was 26 m from the main nest of the colony of *F. polyctena* and about 11 m from its border stations (Fig. 3). In 1987, apart from one *F. fusca* individual seen, no presence of natural slaves was recorded in the colony of *F. sanguinea* (in the previous year they were fairly numerous).

Formica polyctena. This colony, under the symbol K III (Fig. 2), was established in 1986 as one of control colonies which served as objects for investigations on artificial colonization of ants. Soon after the foundation, the colony moved 12 metres farther, getting closer to the then-existing nests of *F. sanguinea* (Fig. 3). The *F. polyctena* nest, intensively supplied with pupae and workers, quickly increased its size and at the time of the studies its dimensions were: $\varnothing = 85$ cm, h = 40 cm. The range of penetration by workers increased, too, and accessory filial nests sprang up spontaneously. In the course of establishing its stations *F. polyctena* also made use of the nests of *F. sanguinea* that had been deserted after the conflict (Fig. 3). Colony K III was highly heterogeneous – it consisted of workers and queens taken from many nests of 4 different polycalic colonies (among these was the colony from which, at a later date, pupae were collected for *F. sanguinea*) and from several monocalic colonies.

Fig. 2. Main nest of the colony of *F. polyctena* K III (its state in 1986; in 1987 the nest was bigger) (photo by W. Czechowski).

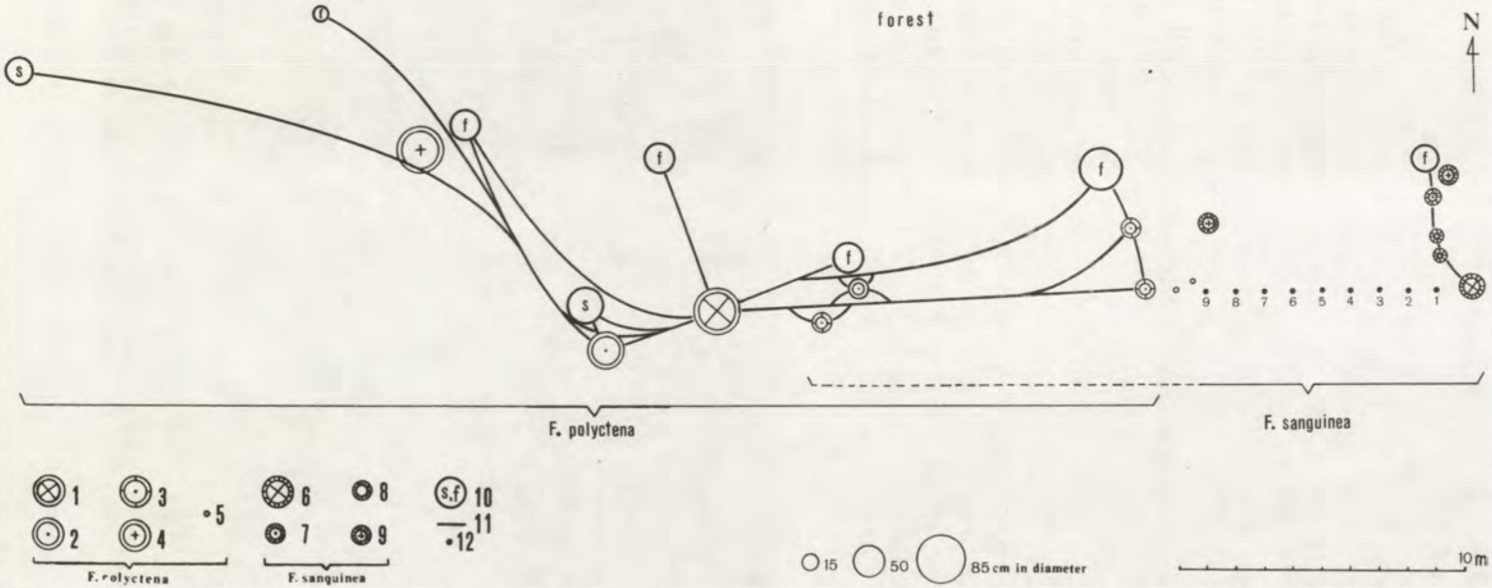

Fig. 3. Situation plan of the study area: 1–5 – objects of *F. polyctena* (1 – main nest, 2 – stations, 3 – stations in abandoned nests of *F. sanguinea*, 4 – first site of artificially founded Colony K III – an abandoned nest, 5 – microstations at permanent natural food sources); 6–9 – objects of *F. sanguinea* (6 – main nest, 7 – filial nest, 8 – initiatory nests, 9 – abandoned nests); 10 – trees invaded by ants (s – spruce, f – fir); 11 – permanent routes of ants; 12 – baits.

METHODS

Pupae from natural nests of *F. polyctena* intended for enriching the colony of *F. sanguinea* were obtained by means of PODKÓWKA'S method (WIŚNIEWSKI 1973). In this procedure apiarian comb frames are inserted into mounds. Pupae were placed in the cells of the combs by ants themselves. When the standard set (3 frames) was used a rich nest could provide, at one go, about 1 dcm^3 of pupae. In the case of the Gorce ecotype of *F. polyctena* (workers are quite small) this meant about 30,000 pupae. After emptying the frames imagines were put aside, the number of pupae was determined by means of the volumetric method, and the pupae were strewn in the immediate vicinity of the nest of *F. sanguinea* (Fig. 4).

From time to time, as slaves began to emerge, random samples of workers were collected from the mixed colony (the surface of the nest was disturbed delicately and ants were picked up from the palm). In this way the varying proportions of each species were determined and at the end of the experiment – when all the known slaves supplied to the *F. sanguinea* colony had left their cocoons – also the absolute abundance of the hosts' swarm was calculated. Moreover, samples of ants performing different tasks were obtained several times

Fig. 4. Colony of *F. sanguinea* (the nest covered with bark) supplied with pupae of *F. polyctena* (the end of July) (photo by W. CZECHOWSKI).

and these were analyzed by means of the chi-square test to see how the proportion of each species in the functional groups of workers varied. The tests were made on the basis of the numbers of individuals (and not on their percentage shares).

In order to provoke confrontations between ants from the mixed colony and the colony of *F. polyctena* (K III) baits with diluted honey were placed between the nests. A series of slaves (about 1000) was marked with the leather dye "Wilbra" to make it easier to distinguish *F. polyctena* individuals of different origin.

DESCRIPTION OF THE EXPERIMENTS AND OBSERVATIONS

Development of the mixed colony

The first pupae of *F. polyctena* were supplied to the colony of *F. sanguinea* at the beginning of July. A vast polycalic colony from Ochotnica Górna, under the symbol S, was the source of pupae. Ants from this colony constituted one of the components of the "artificial" Colony K III adjoining that of *F. sanguinea. F. sanguinea* workers started to pick up the supplied pupae with a violence typical of this species. As the colony began to fill, this violence abated and fewer individuals collected the successive batches of pupae. However, all pupae were always taken, though with larger batches the ants needed several hours. *F. sanguinea* also carried to their nest young, colourless imagines of *F. polyctena* which, when approached by a worker, curled up to be carried. Fully mature individuals were killed at once.

During the period from 12 July to 20 August, the *F. sanguinea* colony was provided with *F. polyctena* pupae 7 times. Together the total of some 230,000 pupae were given, obtained from 8 nests of Colony S (Table 1). The first, relatively small batch of pupae (about 15,000) was absorbed without any difficulty. However, most of the pupae from the next batch (about 40,000) could not be squeezed into a nest filled to its capacity and so the ants placed them in a tuft of grass nearby. To protect the pupae from rain the heap ot pupae was covered with pieces of bark. Very soon, on the same day in fact, *F. sanguinea* workers began to demolish their own nest, and with the material obtained in this way they built a makeshift shelter for alien pupae (!). Within 3 days they pulled down their own mound completely and built a new one above the pupae, at a distance of 20 cm from their previous nest. They also carried there, without any delay, all the pupae they had collected, even those from the underground part of the demolished nest. The new nest kept expanding very rapidly (the process of building was assisted by more and more emerging slaves) and, not without some difficulty, it housed the subsequent batches of pupae supplied.

The fact that *F. sanguinea* abandoned its nest so unexpectedly and easily because of alien pupae, undoubtedly proves that in the ethology of *F. sanguinea*

Table 1. The course of enriching the *F. sanguinea* colony with pupae of *F. polyctena*

Date	Number of sets of frames	Number of pupae	Nest of origin of pupae
12 July	1	15,000	S I
17 July	3	40,000	S IV, S IVA
22 July	4	80,000	S VIII, S VIIIA
1 August	4	45,000	S XIII, S XIV
8 August	1	30,000	S X
12 August	1	10,000	S XIII
20 August	1	10,000	S IV
The whole period	15	230,000	Colony S (8 nests)

the slavery instinct plays the leading part. However, the behaviour was also connected with their lack of attachment to summer nests, something typical of this species (Marikovsky 1967).

The first *F. polyctena* workers appeared on the surface of the nest on 20 July, and their mass emergence took place two days later. This was manifested by a rapidly growing dump of empty cocoons carried out of the nest by *F. sanguinea* workers. Since that moment, on cool, sunny days, the mound was covered with a dense layer of light-coloured, sun-bathing individuals of *F. polyctena* (Fig. 5). As the days passed, more and more of them participated in the usual tasks.

The nest material of *F. polyctena* was put near the colony of *F. sanguinea* together with pupae. (The nest of *F. sanguinea* was situated among dense herbaceous vegetation and the ants had problems with obtaining building material). Gradually, and more and more distinctly the nest took shape of a typical mound of *F. polyctena*. In September its dimensions were: $\varnothing = 40/50$ cm, h = 18 cm. Thus, in comparison with the initial state, the diameter of the nest had increased 2.6 times and the height 3.6 times.

After receiving the third, and the largest, batch of pupae (80,000) the mixed colony started to build branches. First, towards the end of July, two very small branches were made almost simultaneously about 1.5 and 2 m from the nest, towards the edge of the forest (Fig. 3). *F. sanguinea* workers carried thousands of pupae over there (and back). In the light of later developments those stations proved to be the so-called initiatory (trial) nests (Pisarski 1973). Both of them reached the diameter of about 10 cm and they were abandoned the moment a permanent filial nest was built in mid-August. The ants constructed it at 3.5 m from the previous main nest, on the edge of the forest, not far (1 m) from the empty winter nest. This time, the removal (transport of pupae and imagines) was

Fig. 5. Crowds of newly emerged *F. polyctena* workers on the surface of the nest of *F. sanguinea* (photo by W. CZECHOWSKI).

carried out mainly by the *F. polyctena* forces, although no instances were recorded of a slave carrying an imago of the host. It was mainly slaves who built the filial nest, obtaining material from the winter nest demolished for this purpose. In September, the dimensions of the new nest were: $\varnothing = 35$ cm, h = 15 cm. The two nests functioned together for some time, but the old one was being deserted gradually. (Several times it was scratched by a woodpecker). In mid-September, when the observations were concluded, the nest was inhabited only by a few individuals of both species. Both the hosts and the slaves moved from one nest to the other in fairly equal proportions. On 10 September a 1% difference in the proportion of both species in each nest was recorded (in favour of *F. polyctena* in the new one; Table 2), but that difference was statistically insignificant ($\chi^2 = 0.00$).

During the period from 8 August to 12 September, random samples of workers from the main nest were collected 5 times (at 2–20-day intervals). These samples revealed a gradual increase in the proportion of *F. polyctena* in relation to that of *F. sanguinea* in the mixed colony (Table 2). The difference between the first and the last sample was statistically significant ($\chi^2 = 4.10$; $P < 0.05$). The entire series of the 5 catches was statistically heterogenous ($\chi^2 = 9.76$; $P < 0.05$) – this fact will be of importance in further considerations.

Table 2. Changes in the qualitative-quantitative composition of the mixed colony during the experiment

No.	Date	Total number of ants in the sample	Number of individuals of		Proportion of individuals of	
			F. sanguinea	*F. polyctena*	*F. sanguinea*	*F. polyctena*
1	8 August	154	21	133	14%	86%
2	11 August	103	12	91	12%	88%
3	21 August	128	8	120	6%	94%
4	10 September	51	2	49	4%	96%
4a[1]	10 September	(65)	(2)	(63)	(3%)	(97%)
5	12 September	49	2	47	4%	96%

[1] Data for the filial nest.

Towards the end of the observations the proportion of *F. sanguinea* in the mixed colony was 4% and there were no *F. polyctena* pupae there. The number of *F. polyctena* workers could be estimated at about 200,000. Some of the 230,000 pupae provided had to be considered lost, as a result of damage during technical manipulations. A certain number (apart from the damaged ones) may have been devoured by *F. sanguinea*. Plundering pupae for food is a hypothesized origin of slavery in ants (Dobrzański 1965). Some controversy may arise over the assumption about so low, of merely a dozen per cent, losses in pupae and also about the abundance of the swarm of *F. sanguinea* estimated on this basis. There exists information that most (sometimes all) kidnapped pupae of ants outside the subgenus *Serviformica* are eaten by amazon ants. These data refer to *F. rufa* (Dlussky 1967), *F. truncorum* (Marikovsky 1967), *F. pratensis* (Czechowski, unpublished), and *F. exsecta* (Marikovsky 1967). However, certain facts indicate that in the case under discussion the loss of pupae was relatively small. In 1986, the same society of *F. sanguinea* – at that time it was polycalic, much more abundant and in possession of typical slaves (*F. fusca*) – obtained not more than 200–300 *F. polyctena* pupae, as loot from an assault on the newly established Colony K III. It was an insignificant number and yet, later, the presence of imagines of this species in nests of *F. sanguinea* was noticeable. During the studies described here, another colony of *F. sanguinea*, very strong and with slaves (*F. fusca*), which was situated about 50 m from the colony under discussion accidentally obtained a similar-number of *F. polyctena* pupae. In this nest, too, there appeared mature non-specific slaves. That must have been made possible by sufficiently rich food resources of the local habitat.

Assuming that success followed the introduction of 200,000 *F. polyctena* workers (96% of the mixed colony) into the nest of *F. sanguinea* the abundance of the hosts swarm may be estimated at 8,000. It is assumed, of course, that the samples taken were representative of the entire mixed swarm and not only of its part connected with the superficial zone of the nest. It may be presumed, however, that a probable error due to an uneven distribution of the slaves and hosts in the nest was eliminated by the alarm situation sweeping the colony whenever catches were made.

In the case of the mixed colony of *F. sanguinea* + *F. polyctena* in Gorce – even though a filial nest typical of the slave species was built – there were no indications that the swarms would be separated (at least during the first year of the existence of the colony). Such a tendency, however, was manifested by mixed colonies of *F. sanguinea* + *F. rufa* established under similar circumstances in Western Siberia (Marikovsky 1963). In that case, slaves built small filial nests typical of *F. rufa* and these were gradually left by *F. sanguinea*. All that took place during the same season when the mixed society had been formed and as a result a kind of bispecific polycalic colony was formed. In their nests, the ex-slaves treated the vising ex-hosts quite friendly. At the same time, however, they were capable of adopting queens of their own species.

Division of labour

Simultaneously with random samples of workers (with a one-day delay at most) samples of individuals performing particular tasks were collected from the mixed colony. The percentages of *F. sanguinea* and *F. polyctena* were analyzed among ants: 1) picking up the supplied pupae and carrying them into their nest, 2) transporting pupae (and also imagines later on) from the main nest to the newly formed branches, 3) building their nest (transporting and shifting the construction material), 4) making a reconnaissance towards the colony of *F. polyctena* (K III), 5) searching the area around the nest, and 6) visiting aphid colonies in a tree canopy. Samples of all the functional groups, with the exception of scouts, were taken twice or even five times during a period of usually more than a month. The group of scouts is represented by only one sample, because their action took place only once. Theoretically, each sample was to have 50 individuals. This often proved impossible in practice (Table 3), because any interference caused panic among the ants, followed by a long pause in their usual activity.

1. Picking up pupae. Two samples were taken within 4 days when the fifth and sixth batches of pupae were supplied. At that time, the proportion of *F. sanguinea* workers in the entire mixed colony was only 14% and 12%, respectively, and the difference between the random samples from those days was insignificant ($\chi^2 = 0.15$; $P > 0.5$) (Table 2). However, a highly significant difference was found between two samples of the activity under discussion. When the first sample was collected *F. sanguinea* individuals constituted 76% of the ants picking up pupae, and the second time (when, comparatively, there were more of them in the colony) – their share was 90% (Table 3). This difference could not have been due to different wheather conditions during the catches. It is true that the first day was hot and the second cool and wet, but the general thermal requirements of both

species were similar (both of them are mesothermophiles). Moreover, under the local conditions, *F. polyctena* was active longer then *F. sanguinea* when the temperature dropped (thus the results could only be the opposite). In such a situation attention must be drawn to the fact that at the given time the nest was filled with pupae and it could hardly contain the successive batches. It is probable that under such conditions the instinct to protect pupae declines quicker in *F. polyctena* than in *F. sanguinea* in which the drive to acquire pupae is the primary feature of their bionomics (even though in the first case it was their own pupae, and in the second – those of another species). No matter what the difference was between successive samples, the activity of picking up pupae was the only task studied in which the percentage of participating hosts was much higher than that of slaves. It was also the only task in which a significant change was recorded in the proportion of each species in time (Table 3).

2. Transport of pupae and workers. Two samples were taken at an interval of over a month. In the first case pupae were transported to initiatory nests, in the second – workers to a new permanent nest. During the first catch the proportion of *F. sanguinea* in the entire mixed colony was about 14%, during the second only 4% and that difference was statistically significant ($\chi^2 = 4.10$; $P < 0.05$) (Table 2). In spite of this, in both samples of the given functional group of workers the results were almost identical; in total, the proportion of *F. sanguinea* workers in the group of carriers was 22% (Table 3).

3. Nest building. Five samples were taken within a month. During that time the proportion of *F. sanguinea* in the mixed colony decreased from about 14% to 4% and this was statistically significant (χ^2 as above; Table 2). Regardless of the changes in the composition of the entire colony the proportion of workers of each species in the group of builders remained at the same level and the total for *F. sanguinea* was only 2.5% (in relation to the global number of individuals from all samples) (Table 3). [Considering the fact the entire series of samples was statistically homogeneous (Table 3) this way of estimation seems more proper than calculating the mean from the percentages].

4. Reconnaissance. On 9 August, probably as a result of the first contact between individuals of *F. sanguinea* and *F. polyctena* from Colony K III, a violent reaction of the mixed colony was recorded. At midday, in sweltering hot weather, a distinct column of ants marched from the nest of *F. sanguinea* towards the border stations of Colony K III (Fig. 3). The ants behaved as if during a raid, moving very quickly and clearly keeping the direction. Scouts went as far as about 6 m from a station of Colony K III (4 m from their own nest) and there they rapidly penetrated the territory over a small area (less than 1 m²), then returned. At that time, *F. polyctena* workers from the nest of K III were carrying out their usual, dispersed penetration of the area. Encounters were provoked when bait was put out, but did not happen spontaneously. The group of scouts was slightly dominated by *F. sanguinea* individuals which constituted 52% of all (Table 3). In

Table 3. Proportions of *F. sanguinea* and *F. polyctena* individuals from the mixed colony in particular functional groups of workers – data from successive samples

Task	Date	Total number of ants in the sample	Number (and %) of individuals of		Degree of differentation
			F. sanguinea	*F. polyctena*	
Picking up pupae	8 August	51	39 (76%)	12 (24%	highly significant;
	12 August	50	45 (90%)	5 (10%)	($\chi^2 = 46.00$; $P < 0.001$)
Transport of	9 August*	31	7 (23%)	24 (77%)	insignificant;
pupae* or workers**	12 September**	36	8 (22%)	28 (78%)	($\chi^2 = 0.00$, $P > 0.05$)
Nest building	9 August	51	1 (2%)	50 (98%)	
	11 August	15	– (0%)	15 (100%)	insignificant;
	21 August	73	3 (4%)	70 (96%)	($\chi^2 = 1.56$; $P > 0.05$)
	10 September	20	– (0%)	20 (100%)	
Reconnaissance	9 August	42	22 (52%)	20 (48%)	
Searching the area	11 August	38	6 (16%)	32 (84%)	
	21 August	46	8 (17%)	38 (83%)	insignificant;
	10 September	32	5 (16%)	27 (84%)	($\chi^2 = 0.34$; $P > 0.05$)
	12 September	42	6 (14%)	36 (86%)	
Visiting aphids	9 August	93	5 (5%)	88 (95%)	
	11 August	36	4 (11%)	32 (89%)	insignificant;
	21 August	60	2 (3%)	58 (97%)	($\chi^2 = 3.64$; $P > 0.05$)
	10 September	55	5 (9%)	50 (91%)	
	12 September	56	4 (7%)	52 (93%)	

the entire mixed colony *F. sanguinea* ants constituted, at that time, merely about 14% (Table 2).

5. Searching the area. After the above-described reconnaissance the penetration of the border area by ants from the mixed colony was fairly animated. No doubt, that situation was maintained artificially by luring ants to baits. (Without this it would have been impossible to collect samples with the required abundance, and that was made plain when the untouched area on the opposite side of the *F. sanguinea* nest was searched). The penetrating ants were picked up over a limited section of the area, between 2 and 4 m from the *F. sanguinea* nest, in order to avoid incidental catches of *F. polyctena* individuals from Colony K III. No catches were made during periods of occasional conflicts between ants from neighbouring nests. During a month, 4 samples were taken and it was found out that among the penetrating ants the percentage of the hosts (16%, in general) and the slaves was stable (Table 3). During the same period it was recorded for the entire mixed colony that the proportion of *F. sanguinea* dropped from 12% to 4%, but the differentation in the distribution of the numbers of individuals of both species in particular random samples was not significant statistically ($\chi^2 = 3.09$; $P > 0.05$) (Table 2).

6. Visiting aphids. Before the experiments, when the future mixed colony was still a conspecific swarm of *F. sanguinea*, there were no records of *F. sanguinea* foragers climbing the nearby trees. When the abundance of the colony increased rapidly, there appeared a distinct food trail to the nearest fir-tree (Fig. 3), gradually expanding. In August and September, in favourable weather, the intensity of the foraging traffic along the trunk of that tree reached 50 individuals per minute (in one direction). During a period of over a month, 5 samples of foragers were collected. The series proved to be statistically homogeneous; the share of *F. sanguinea* in the group visiting aphids was 7% in all (Table 3). At that time the proportion of *F. sanguinea* in the entire colony decreased from about 14% to 4% and that change was statistically significant ($\chi^2 = 4.10$; $P < 0.05$) (Table 2).

As the above data show, the colony of *F. sanguinea* + *F. polyctena* maintained a surprisingly stable percentage of each species in particular functional groups of workers, in spite of their increasing quantitative disproportion in the entire mixed swarm. That was the case in 5 out of 6 analyzed functional groups. However, in relation to each other the proportions of *F. sanguinea* and *F. polyctena* in particular groups differed greatly: from, respectively, 83%:17% (picking up pupae) to 2.5%:97.5% (nest building) (Table 4). In this respect, the pool of the functional groups studied was characterized by heterogeneity of high statistical significance ($\chi^2 = 332.53$; $P < 0.001$). The following rule applied: the more a given function was connected (either directly as when picking up pupae or indirectly as during reconnaissance) with the practice of obtaining slaves, the greater was the involvement of *F. sanguinea* individuals. In functions of a general nature (nest building, visiting aphids) their percentage was minimal (Table 4).

Table 4. Proportions of *F. sanguinea* and *F. polyctena* individuals from the mixed colony in particular functional groups of workers – comprehensive data arranged according to the decreasing participation of *F. sanguinea*

Task	Total number of ants in all the samples	Number (and %) of individuals of	
		F. sanguinea	*F. polyctena*
Picking up pupae	101	84 (83%)	17 (17%)
Reconnaissance	42	22 (52%)	20 (48%)
Transport of pupae or workers	67	15 (22%)	52 (78%)
Searching the area	158	25 (16%)	133 (84%)
Visiting aphids	300	20 (7%)	280 (93%)
Nest building	159	4 (2.5%)	155 (97.5%)

When the compositions of particular functional groups were compared after a formula "each with all the others" it was confirmed that they differed greatly in relation to one another. Out of 15 possible combinations, the difference was insignificant only in two cases (transport of pupae/searching the area and nest building/visiting aphids). In all the other cases the differentation was statistically very significant (Table 5).

In 5 cases out of the 6 functions analyzed (with the exception of tending aphids) it was found out that in the composition of particular functional groups there were statistically significant deviations from the existing composition of the entire mixed colony (Table 6).

Table 5. Differentiation in the proportions of *F. sanguinea* and *F. polyctena* individuals from the mixed colony in particular functional groups of workers (the critical value χ^2 at $P = 0.05$ is 3.84: – – an insignificant difference, + – $P < 0.05$, ++ – $P < 0.01$, +++ – $P < 0.001$)

	Picking up pupae	Transport of pupae or workers	Nest building	Recon-naissance	Searching the are	Visiting aphids
Picking up pupae		+++	+++	+++	+++	+++
Transport of pupae or workers	58.99		+++	+++	–	+++
Nest building	262.32	21.61		+++	+++	–
Reconnaissance	14.17	11.09	81.46		+++	+++
Searching the area	111.81	1.30	18.39	23.98		++
Visiting aphids	232.51	17.92	3.17	74.52	8.72	

Upper right (signs): Degree of differentiation; lower left (numbers): χ^2 values

Table 6. Differentiation in the proportions of *F. sanguinea* and *F. polyctena* individuals in each of the functional groups of workers in relation to the actual proportions of individuals of these species in the entire mixed colony (based on a compilation of data from Tables 2 and 4; symbols as in Table 5)

Task	χ^2	Degree of differentiation
Picking up pupae	163.06	+++
Transport of pupae of workers	6.07	+
Nest building	9.36	++
Reconnaissance	30.28	+++
Searching the area	8.35	++
Visiting aphids	1.80	–

Relations with the colony of *F. polyctena*

The attitude of *F. polyctena* ants towards slaves of *F. sanguinea* of the same species was initially studied in 1986. At that time, and in the following year, slaves were confronted with "free" workers of *F. polyctena* when the former were planted within the colony (K III) of the latter. In 1986, slaves were directly derived from Colony K III and in 1987 they were indirectly connected with it genetically (see the chapter: "Objects of the study"). Moreover, each time *F. polyctena* pupae were delivered to the nest of *F. sanguinea* some pupae (about one-fourth of the number of given *F. sanguinea*) were dropped near the border stations of Colony K III. Thus, a certain amount of workers from the current swarm of that colony were sisters to the slaves of *F. sanguinea*.

The reactions of confronted ants were not explicit (in the two years). The enslaved individuals of *F. polyctena* faced different reactions of members of Colony K III – from definite aggression to almost indifference. The extreme reactions were very rare. Most frequently it was nervous curiosity. Usually a few workers caught the intruder by its antennae and legs, it was immobilized and studied with great interest for several or several dozen minutes. Gradually, the curiosity of the attackers abated, they left one by one and the intruder was free. If it had not been seriously injured by some particularly excited attacker, it could move quite freely among the alien ants. The above reactions were recorded both on the surface of the mound of Colony K III and near border stations. Intruders were often pulled into the nest and, for obvious reasons, their fate remained unknown. It is worth mentioning here that an alien ant that had been put artificially within the territory of a foreign nest incited greater aggression in the host individuals than it would have during more natural encounters (during the so called "busy walks" of the partners) (Marikovsky 1963).

The number of the above experiments was not sufficient to make possible a quantitative analysis of the reactions of ants. There is no doubt, however, that the enslaved individuals of *F. polyctena* from the nest of *F. sanguinea* were received by the colony of *F. polyctena* far less aggressively than their holders – the amazon ants. In the same circumstances, *F. sanguinea* workers were attacked at once and with such fury that there could be no illusions about their fate.

In that situation it was attempted to provoke an encounter of individuals from the studied colonies as a result of increasing their range of penetration. To this aim, both societies were provided with pupae at the same time. It is true that all pupae supplied to the border stations of Colony K III were always carried by ants to the main nest, but these manipulations were accompanied by such a stir near the stations that they were expended and their staff reinforced; thus increased the range of workers penetrating the border zone.

The plan was successful – the ants made contact which was first manifested by the previously described reconnaissance raid of the mixed colony. This raid, undoubtedly inspired by *F. sanguinea* and conducted with its numerical advantage, may have decided the future (moderately) hostile relations between *F. polyctena* ants from both colonies.

The raid (9 August) took place between 11.00 and 13.00 and just before 13.00 it slackened. At that moment, a row of baits (every 1 m) with diluted honey was placed between the nest of *F. sanguinea* and a border station of *F. polyctena* (Fig. 3). This led, but only at 17.30, to the first conflict between the ants. It occurred near Bait 4 and that was a place that had been reached by the raid of *F. sanguinea* + *F. polyctena*. Direct skirmishes involved not more than about 100 individuals on each side. In the evening, the conflict was over. On the following day, and on several successive days, foragers from the mixed colony utilized only Bait 1 (the closest to their nest) and near the other baits penetration by ants (from both colonies) was dispersed and almost without conflict. At that time, the baits were refilled systematically because they were used intensively by *Myrmica laevinodis* ants, by bees, bumble-bees, wasps, flies, and butterflies. It was also then that some 1,000 slaves were marked in the mixed colony. The next obvious, yet not very serious conflict occurred on 17 August, near Bait 6. After 20 August, there were no more conflicts. Since the attitude of *F. polyctena* from Colony K III was passive, the border line was established between Baits 8 and 9, that is in a place where the range of penetration by *F. polyctena* workers from their border stations ended (Fig. 3). The border was flexible and it seems that it was trespassed by *F. polyctena* on both sides. Its approximate course was decided by the range of penetration by the marked individuals from the mixed colony. Although there were unmistakable cases of peaceful contacts between ants from both colonies no instances were recorded when slaves (the marked ones) would go to Colony K III (the presence of marked individuals in the border area was conspicuous).

In battles, the forces of the mixed colony consisted of slaves fighting alongside *F. sanguinea* ants. Towards their conspecific enemies the slaves seemed to be more aggressive than the former towards them. After the first conflict, dead ants were collected from among those carried by *F. polyctena* to Colony K III. Out of 26 dead ants 16 belonged to *F. sanguinea*. Among 10 dead *F. polyctena* 3 were attached by their mandibles to dead *F. sanguinea* – this meant that they were individuals from Colony K III. Thus, on the side of the mixed colony, only 30% (and probably the number was much lower) of casualties were slave *F. polyctena* individuals. In the raid preceding the conflict the numbers of both species were more or less the same (Table 3). During the subsequent battle the percentage of the slaves was practically at least on the same level. It is easier for fighting *F. polyctena* ants to kill a conspecific opponent than a *F. sanguinea* worker (this was manifested in numerous observations). These premisses lead to a conclusion (very cautious, of course, because of few quantitative data) that, while fighting with the mixed colony, *F. polyctena* workers from Colony K III attacked *F. sanguinea* workers rather than the conspecific slave individuals. (If they had chosen their victims at random, there should have been a much greater number of *F. polyctena* individuals among the casualties on the side of the mixed colony).

At the time when encounters were bound to happen, some *F. sanguinea* workers (as excited as the rest) carried dead ants (of their own species or of slaves) from their nest to the conflict area. The usual rubbish heaps were somewhere else. Sometimes the rate of that carrying of dead ants was 10 per 10 minutes. This never happened in a quiet colony. This phenomenon suggests that, in conflict situations, in ants, their own dead individuals are associated with some signalling message; that was not the first observation of the kind. The previous ones also referred to *F. sanguinea* (vs *F. cinerea* Mayr) and *Lasius niger* (vs *Myrmica laevinodis*) (Czechowski 1975, 1977, 1985).

In the picture of the relations between the colonies a "reluctance" of both sides to engage in an open conflict was clearly marked – even though the ants were constantly provoked (baits), even though *F. sanguinea* is known for its immoderate aggression towards species of the *F. rufa* group as its most dangerous competitor (Marikovsky 1963), and although (maybe just because of the fact that) the recent past of both societies abounded in drastic contests exterminating to the two sides. It seems that the causes of the development of such mutual attitudes must be sought in the very history of their previous relations and in the given trophic situation of each colony.

It must be remembered that the *F. sanguinea* colony under discussion was a remnant of a former, very strong polycalic society. Its regression (and territorial shift) resulted from a long-lasting conflict with Colony K III. That conflict, initiated by *F. sanguinea*, first threatened the existence of the colony of *F. polyctena*. Only the interference of the author (see the chapter "Objects of the study") led to a change in the distribution of forces. The artificially expanding Colony K III was very active in forcing *F. sanguinea* swarms out of their nests, but later the mere presence of the dangerous partner in the neighbourhood was enough to make them migrate. (The last nest was deserted in the spring of the research season; Fig. 3). The subsequent severe defeats must have remained in the "memory" of the *F. sanguinea* society and the recorded abatement in its tendency to fight with such a dangerous opponent ought to be treated as a manifestation of the ecological plasticity of the species. In similar situations, colonies of *Polyergus rufescens* Latr., a social parasite with a far more ritualized behaviour, are completely annihilated (Dobrzańska, Dobrzański 1962, Dobrzański, Dobrzańska 1975).

It is a fact, however, that *F. sanguinea* was the more aggressive and expansive participant in the conflict under discussion. It occupied 8 out of the 9 baits provided, moving to the immediate neighbourhood of the territory of *F. polyctena*. But the last two baits (N° 7 and 8) were taken over without combat at a time when *F. polyctena* workers were no longer interested in them (Bait 9 practically belonged to no one). The "success" of *F. sanguinea* (or, to be precise, of the mixed colony) may have been decided by the following factors: a considerable increase in the abundance of the colony which, on the one hand, gave *F. sanguinea* ants a sense of strength and, on the other, forced them to look for new sources of food, and the surrender (this factor was probably more important) *F. polyctena* ants from Colony K III.

That surrender of *F. polyctena* probably expressed the economics of the functioning of the colony. Unlike the mixed colony, Colony K III was stable in abundance (the extra batches of pupae mattered little against the huge abundance of the colony) and it utilized permanent, rich (and safe) food sources (Fig. 3). In that situation losses caused by the conflict would undoubtedly have exceeded advantages if the baits had been taken over. It is true that *F. polyctena* foragers started to exploit the baits, but they abandoned them almost the moment they met on their way *F. sanguinea* workers – dangerous opponents in any case. Not without consequence was also the fact that *F. polyctena*, unlike *F. sanguinea*, is a typically territorial species. Most probably all the baits were situated beyond the border of the territory of Colony K III, and they certainly were beyond the zone of intensive penetration. It cannot be ruled out that the presence of the slaves of *F. sanguinea*, conspecific to Colony K III, played a buffer role which pacified the fighting attitudes of both sides.

In the light of the phenomena recorded it cannot be stated for a fact that the change in the status of *F. polyctena* workers (they were made slaves to another species) increased the directed at them (and vice versa) aggressiveness of "free" alien ants of their own species. Intercolonial intraspecific relations in ants of the *F. rufa* group develop in different ways – from peaceful unions of foreign swarms to long-lasting, drastic conflicts. Cases are known of temporary mutual cannibalistic predation between colonies within polycalic societies (Mabelis 1979, 1984 Vepsäläinen, personal communication). During the work on artificial colonization of *F. polyctena* in the Gorce Mts. it was found out (taking, among others, Colony K III as an example) that the reaction of an existing colony to a new one, established in the vicinity, can vary a lot. It happened that totally alien swarms joined without any conflict while branches taken at different time intervals from the mother colony wage a long, fierce war. However, in all the cases recorded (and there were many of them) even very "bloody" conflicts lasting for many days were finished in a union of the swarms or in establishing peaceful relations between them (the author's unpublished data). Therefore it is difficult to predict how the relations between Colony K III and the conspecific slaves from the mixed colony would have developed if the intensive contacts (even the hostile ones) between them had lasted longer.

RECAPITULATION

1. *F. polyctena* workers are potentially fully accepted slaves in colonies of *F. sanguinea*. Of course, such mixed colonies occur extremely seldom because, under ordinary conditions, *F. sanguinea* has hardly any opportunities to obtain pupae of this species.

2. A colony of *F. sanguinea* is practically able to receive any number of pupae of the slave species, even if this involves moving to a new nest. The experimentally made mixed colony of *F. sanguinea* + *F. polyctena* consisted in 96% of slaves (about 200,000 individuals).

3. In a mixed colony of *F. sanguinea* + *F. polyctena* work is divided between the slave-holders and slaves. The shares of each species in carrying out particular tasks are different from their percentages in the composition of the entire colony. When the numerical advantage of slaves is very great the shares remain the same, regardless of the increasing disproportion between the number of slaves and their holders in the colony.

4. In the above situation, the percentage of *F. sanguinea* in a particular functional group of workers increases the closer function the connection of given with the task of obtaining pupae (picking up pupae – 83%, reconnaissance – 52%, transporting pupae during removal – 22%, searching the area – 16%, collecting honeydew – 7%, nest building – 2.5%).

5. During a conflict between the mixed colony of *F. sanguinea* + *F. polyctena* with the colony of *F. polyctena* the slaves fight on the side of their holders. However, towards them the aggressiveness of "free" *F. polyctena* workers is weaker than that towards *F. sanguinea* individuals.

6. The mutual aggressiveness of *F. polyctena* workers from an ordinary colony and of conspecific slaves of *F. sanguinea* remains within the variability limits of the degree of mutual aggressiveness of different polygynic colonies in this species.

REFERENCES

CZECHOWSKI W. 1975. Wyprawy rabunkowe *Formica* (*Raptiformica*) *sanguinea* LATR. (*Hymenoptera, Formicidae*). Prz. zool., Wrocław, **19**: 33–43.

CZECHOWSKI W. 1977. Recruitment signals and raids in slave-maker ants. Ann. zool., Warszawa, **34**: 1–26.

CZECHOWSKI W. 1985. Competition between *Myrmica laevinodis* NYL. and *Lasius niger* (L.) (*Hymenoptera, Formicoidea*). Ann. zool., Warszawa, **39**: 153–173.

CZECHOWSKI W. 1989. Kolonizacja mrówki ćmawej (*Formica polyctena* FOERST.; *Hymenoptera, Formicicidae*) w górnoreglowych drzewostanach świerkowych Gorczańskiego Parku Narodowego uszkodzonych żerem zasnui wysokogórskiej (*Cephalcia falleni* DALM.; *Hymenoptera, Symphyta*). Wiad. entomol., Warszawa (in print).

DLUSSKY G. M. 1967. Murav'i roda Formika (*Hymenoptera, Formicidae*, g. *Formica*). Izd. "Nauka", Moskva, 236 pp.

DOBRZAŃSKA J., DOBRZAŃSKI J. 1962. Quelques observations sur les luttes entre différentes espèce de fourmis. Acta Biol. exp., Warszawa, **22**: 269–277.

DOBRZAŃSKI J. 1965. Genesis of social parasitism among ants. Acta Biol. exp., Warszawa, **25**: 59–71.

DOBRZAŃSKI J., DOBRZAŃSKA J. 1975. Ethological studies in the ant *Tetramorium caespitum* MAYR. II. Interspecific relationships. Acta Neurobiol. exp., Warszawa, **35**: 311–317.

MABELIS A. A. 1979. Wood ant wars. The relationship between aggression and predation in the red wood ant (*Formica polyctena* FÖRST.). Nether. J. Zool., Leiden, **29**: 451–620.

MABELIS A. 1984. Aggression in wood ants (*Formica polyctena* FOERST., *Hymenoptera, Formicidae*). Aggress. Behav., New York. N. Y., **10**: 47–53.

MARIKOVSKY P. I. 1963. The ants *Formica sanguinea* LATR., as pillagers of *Formica rufa* LIN. nests. Insectes soc., Paris, **10**: 119–128.

MARIKOVSKY P. I. 1967. Biologija murav'ja *Formica sanguinea* LATR. (*Hymenoptera, Formicidae*) v uslovijach Tjan'- Šanja, Ènt. Obozr., Moskva, **46**: 81–91.

PISARSKI B. 1973. Struktura społeczna *Formica* (*C.*) *exsecta* NYL. (*Hymenoptera*: *Formicidae*) i jej wpływ na morfologię, ekologię i etologię gatunku. IZ PAN, Warszawa, 134 pp.

PISARSKI B., VEPSÄLÄINEN K. 1984. Social dominance hierarchy as the basis of ant community structure. In: Proc. 27th Intern. Congr. Entomol., Hamburg.

PISARSKI B., VEPSÄLÄINEN K. 1989. Competitive hierarchy in ant communities (*Hymenoptera, Formicidae*). Ann zool., Warszawa, **42**: 321–329.

SAKAGAMI S. F., HAYASHIDA K. 1962. Work efficiency in heterospecific ant groups composed of hosts and their labour parasites. Anim. Behav., London, **10**: 96–104.

SAVOLAINEN R., VEPSÄLÄINEN K. 1988. A competition hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos, Copenhagen, **51**: 135–155.

STITZ H. 1914. Die Ameisen (*Formicidae*). In: Die Insecten Mitteleuropas insbesondere Deutschlands. II. Hymenopteren (ed. Chr. SCHRÖDER). Stuttgart, pp. 1–111.

WHEELER M. W. 1910. Ants. Their structure, development and behaviour. Columbia Univ. Press, New York, 25 + 663 pp.

WIŚNIEWSKI J. 1973. Badania nad przydatnością patentu PRL Nr 54123 w sprawie pobierania poczwarek z mrowisk. Pr. Kom. Nauk roln. leśn. Pozn. TPN, Poznań, **36**: 247–250.

Instytut Zoologii PAN
ul. Wilcza 64
00-679 Warszawa, Poland

STRESZCZENIE

[Tytuł: Funkcjonowanie mieszanego mrowiska *Formica sanguinea* LATR. + *F. polyctena* FOERST. (*Hymenoptera, Formicidae*) w warunkach nadmiaru niewolnic]

Eksperymenty przeprowadzono w r. 1987 w Ochotnicy Górnej przy okazji prac nad sztuczną kolonizacją mrówek z grupy *Formica rufa* L. w Gorcach (Beskidy Zachodnie). Do monokalicznego mrowiska *F. sanguinea*, liczącego ok. 8 tys. osobników, wprowadzono (partiami) przeszło 200 tys. poczwarek robotnic *F. polyctena*. Uzyskano mrowisko mieszane, złożone w 96% z niewolnic nietypowego gatunku. Badano reakcje *F. sanguinea* na tę sytuację, rozwój mieszanego mrowiska, podział pracy w jego obrębie oraz stosunki z pobliskim – sztucznie założonym, ale w pełni ustabilizowanym – mrowiskiem *F. polyctena*. Stwierdzono, że:

1. Robotnice *F. polyctena* potencjalnie są w pełni akceptowanymi niewolnicami w mrowiskach *F. sanguinea*. (Takie mieszane mrowiska zdarzają się oczywiście niezmiernie rzadko, gdyż w normalnych warunkach *F. sanguinea* ma znikome możliwości pozyskania poczwarek tego gatunku.)

2. Mrowisko *F. sanguinea* praktycznie jest w stanie przyjąć każdą liczbę poczwarek gatunku niewolniczego, nawet jeśli wiąże się to z koniecznością rozebrania własnego gniazda celem zabezpieczenia nie mieszczących się w nim obcych poczwarek.

3. W mieszanym mrowisku *F. sanguinea* + *F. polyctena* obowiązuje podział pracy między gospodarzy gniazda i niewolnice. Udziały każdego z gatunków w spełnianiu określonych czynności są różne od ich proporcji w składzie całego mrowiska. W warunkach dużej przewagi liczebnej niewolnic udziały te pozostają stałe, niezależnie od rosnącej dysproporcji między liczbą niewolnic i gospodarzy w mrowisku.

4. W sytuacji jw., udział *F. sanguinea* w określonej grupie funkcyjnej robotnic jest tym większy, im dana czynność jest bardziej związana z procederem pozyskiwania niewolnic (zbieranie dostarczonych poczwarek – 83%, zwiad – 52%, przenoszenie poczwarek i imagines podczas przeprowadzki – 22%, penetracja terenu – 16%, zbieranie spadzi – 7%, budowa gniazda – 2,5%).

5. Podczas konfliktu mieszanego mrowiska *F. sanguinea* + *F. polyctena* z mrowiskiem *F. polyctena* niewolnice walczą po stronie pasożyta (nawet, jeśli są genetycznie spokrewnione z konspecyficznym przeciwnikiem). Agresywność "wolnych" mrówek *F. polyctena* jest jednak wobec nich mniejsza niż wobec osobników *F. sanguinea*.

6. Obopólna agresywność robotnic *F. polyctena* z normalnego mrowiska i konspecyficznych im niewolnic *F. sanguinea* mieści się w granicach zmienności stopnia wzajemnej agresywności różnych poliginicznych mrowisk tego gatunku.

РЕЗЮМЕ

[Заглавие: Функционирование смешанного муравейника *Formica sanguinea* Latr. + *F. polyctena* Foerst. (*Hymenoptera*, *Formicidae*) в условиях избытка рабов]

Эксперименты были проведены в 1987 году в Охотнице-Гурной при случае искуственной колонизации муравьев из группы *Formica rufa* L. в Горцах (Западные Бескиды). В монокальный муравейник *F. sanguinea*, насчитывающий около 8 тыс. особей вселили (партиями) свыше 200 тыс. куколок рабочих *F. polyctena*. Таким образом получился смешанный муравейник, состоящий в 96% из рабов нетипичного вида. Исследовали при этом реакции *F. sanguinea*, развитие смешанного муравейника, разделение труда в его пределах и отношения с близьлежащим, искусственно созданным, но вполне стабильным муравейником *F. polyctena*. Констатировали, что:

1. Рабочие *F. polyctena* могут вполне акцептироваться рабами в муравейниках *F. sanguinea*. (Совершенно очевидно, что такого рода смешанные муравейники встречаются чрезвычайно редко, поскольку в нормальных условиях возможности *F. sanguinea* раздобыть куколки *F. polyctena* весьма малы).

2. Муравейник *F. sanguinea* может принять практически каждое количество куколок вида рабов, даже в том случае, если это связано с необходимостью разобрать собственное гнездо с челью обеспечения не помещающихся в нем куколок.

3. В смешанных муравейниках *F. sanguinea* + *F. polyctena* обязывает разделение труда между хозяевами гнезда и рабами. Участие каждого из видов в исполнении определенных функций не соответствуют их пропорциям в составе всего муравейника. В условиях значительного численного перевеса рабов эти соотношения остаются постоянными, независимо от возрастающей диспропорции между числом рабов и хозяевов в муравейнике.

4. В описанной ситуации участие *F. sanguinea* в группе несущей определенные функции тем выше чем более данная деятельность связана с промыслом рабов (собирание доставленных куколок — 83%, разведка — 52%, перенесение куколок и имаго во время переселения — 22%, проникновение на территорию — 16%, сбор пади — 7%, постройка гнезда — 2,5%).

5. Во время столкновений смешанного муравейника *F. sanguinea* + *F. polyctena* с муравьйником *F. polyctena* рабы борятся по стороне хозяев (даже в случае генетического родства с конспецифическим противником). Однако агрессивность по отношению к ним „свободных" муравьев *F. polyctena* меньше, чем по отношению к особям *F. sanguinea*.

6. Взаимная агрессивность рабочих *F. polyctena* из нормального муравейника и конспецифических им рабов *F. sanguinea* находится в границах изменчивости степени взаимной агрессивности разных полигинных муравейников этого вида.

Redaktor pracy – prof. dr hab. B. Pisarski