

Emancipation of Slaves in *Formica sanguinea* Latr. Colonies (Hymenoptera, Formicidae)

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Abstract. *Formica sanguinea* Latr. occasionally takes wood ants as its slaves. Eleven nests of the former were experimentally provided with various amounts (10,000–250,000) of pupae of *F. polyctena* Foerst. or *F. rufa* L., and thus, mixed colonies with different proportions of slaves (29–96%) were obtained. The slaves destroyed the *F. sanguinea* colonies by eliminating their brood and queen(s) (with no aggressiveness towards adult workers). The following year, even though *F. sanguinea* workers were still present, the slaves adopted young queens of their own species. Before their complete emancipation, the slaves fought on the side of the slavers during conflicts with conspecific ants, even against their former nestmates. Emancipation restored mutual comity between the ex-slaves and the unenslaved *F. polyctena*. At the same time, the ex-slavers lost their aggressiveness towards alien *F. polyctena* (but not vice versa). The mixed colonies were raided by foreign *F. sanguinea*. The studies were carried out in the Gorce Mts (the Western Carpathians) from 1987 to 1991.

Key words: *Formica sanguinea*, wood ants, social parasitism, dulosis, mixed colonies, queen adoption, nest takeover, aggressiveness, colony odour

INTRODUCTION

Formica (*Raptiformica*) *sanguinea* Latr. is a common northern-Palaeartic slave-maker. Ants of the subgenus *Serviformica* For. are its typical slaves. Occasionally, however, particularly in Central Europe, this function is fulfilled by wood ants (the subgenus *Formica* s. str.) (Stitz 1914, Donis-

thorpe 1915, Wheeler 1926, Forel 1928, Dobrzański 1961, Kutter 1968, Czechowski 1975a) or by another ant species. Such atypical slaves, *F. pratensis* Retz. and *F. polyctena* Foerst., were found during recent studies on the myrmecofauna of Polish pine forests (Tucholskie Forests, Biała Forest) in two out of about 80 (2.5%) recorded nests of *F. sanguinea* (Czechowski *et al.* 1995). Their shares in the mixed colonies were over a dozen percent (Czechowski, Pisarski, unpubl. data). Podkówek (pers. comm.)

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Table 1. Range, course and results of the experiments on slave emancipation in *Formica sanguinea* colonies

Colony	Original numbers of <i>F. sanguinea</i>	Start of the experiment	Pupae introduced		Proportion of slaves in autumn (%)
			numbers	species	
SP-I	8,000	1987	230,000	<i>F. polyctena</i>	96
SP-II	50,000	1988	250,000	<i>F. polyctena</i>	80
SP-III	20,000	1989	25,000	<i>F. polyctena</i>	52
SP-IV	50,000	1989	110,000	<i>F. polyctena</i>	66
SP-V		1989	15,000	<i>F. polyctena</i>	
SP-VI	4,000	1989	30,000	<i>F. polyctena</i>	85
SP-VII	10,000	1989	50,000	<i>F. polyctena</i>	88
SP-VIII	40,000	1989	20,000	<i>F. polyctena</i>	29
SP-IX	2,000	1990	10,000	<i>F. polyctena</i>	82
SP-X	5,000	1990	50,000	<i>F. polyctena</i>	90
SR-I	4,000	1989	15,000	<i>F. rufa</i>	77
SF-I	?	1989	20,000	<i>F. fusca</i>	36

observed numerous natural colonies of *F. sanguinea* mixed with *F. pratensis* at Prószków (Silesia), as well as with ants of the subgenus *Coptoformica* Müll. at Złocieniec (Pomerania). Gallé (pers. comm.) saw even *Camponotus fallax* (Nyl.) as *F. sanguinea* slaves in Hungary. No phenomena like these seem to occur in other regions [Finland: Rosengren *et al.* (1986); Siberia: Bugrova, pers. comm.]. There may be some zoogeographic regularity in this case because, for instance, in Great Britain (this country being the limit of the range of the species), *F. sanguinea* takes advantage of slaves (even typical ones) to a lesser degree than in Central Europe (Darwin 1859, Sudd, Franks 1987). A similar situation occurs in Central Asia (Tien Shan Mts; Marikovskiy 1963) – an area of isolated populations of the species.

The abundance of slaves in *F. sanguinea* nests depends on colony size and on the availability of potential prey; *F. sanguinea* appears to show a

tendency to take unlimited numbers of alien pupae supplied (Czechowski 1989, 1990a). [Marikovskiy (1963), however, reported that the pillaging activity of *F. sanguinea* weakened when there was a lot of slaves present in their nests]. This very greed of the slavers turns against them when wood ants, for instance *F. pratensis* (Forel 1874, 1928) or *F. polyctena* (Czechowski 1990a), are their slaves. These, when occurring in great numbers, destroy an entire *F. sanguinea* colony by eliminating its queen(s) and brood. Later, they adopt young conspecific queens and the colony of *F. sanguinea* is gradually transformed into an ordinary colony of the former victim (Czechowski 1990a). A different scenario is also possible, as the one described by Marikovskiy (1963) from Western Siberia, with *F. rufa* L. as a slave species: swarms of slaves and slavers were separated and this led to the origin of something like a bispecific poly(oligo-?)calic colony.

The present paper is a continuation of earlier studies (Czechowski 1989, 1990a,b). The objective was to investigate the phenomenon of slave emancipation¹ in a quantitative aspect, into the concomitant changes in the ant behaviour and to possibly explain the discrepancies between the observations of Forel and the author on the one hand, and those of Marikovskiy on the other.

¹ The term "slaves" used for these individuals may seem inappropriate because of their species status not typical of ordinary slaves, their enormous relative abundance, which usually highly exceeds that of the *F. sanguinea* colonies, and the artificial manner in which these ants entered a given colony (and also their fatal impact). The term "emancipation" used to define the phenomenon described is controversial, too. However, it is difficult to find justification for abandoning the traditional term "slaves". Wood ants can be slaves of *F. sanguinea* under natural conditions, the typical (and natural) slaves (*Serviformica*) occasionally have an abundance highly exceeding that of the colony of their parasite, and the very difference in the manner in which foreign pupae get into a nest of *F. sanguinea* (natural kidnapping and experimental introduction) cannot be a sufficient reason for treating both groups as different qualitative categories. The term "emancipation" is therefore simply the logical consequence of keeping the term "slaves"

Proportion of <i>F. sanguinea</i> the next year (%)			Adoption of new queens	Colony status the following years (till 1991)
spring	summer	autumn		
0	0	0	+	pure <i>F. polyctena</i>
<1	0	0	+	pure <i>F. polyctena</i>
3	0	2	+	mixed <i>F. polyctena</i> + <i>F. sanguinea</i>
5	3	0	+	pure <i>F. polyctena</i>
8	3	?	+	pure <i>F. polyctena</i>
9	colony included to Colony SP-III			
23	13	?	?	stroyed by foreign <i>F. sanguinea</i>
0	?	?	+	pure <i>F. polyctena</i>
<1	?	?	+	pure <i>F. polyctena</i>
<1	0	0	+	mixed <i>F. rufa</i> + <i>F. polyctena</i>
80	?	?	-	normal <i>F. sanguinea</i> + slaves

STUDY AREA, MATERIAL, METHODS

The studies were carried out in the Jaszcz stream valley (locality of Ochotnica Górna) in the Gorce Mts (the Western Carpathians, southern Poland) from 1987 to 1991. The experiments were conducted on 11 colonies of various sizes (2,000–50,000 individuals) of *F. sanguinea*, which were provided with different numbers (10,000–250,000) of pupae of *F. polyctena* workers (10 cases; Colonies SP-I–X) or *F. rufa* ones (Colony SR-I). [Some findings (data from Colonies SP-I and SP-II) were published earlier as a preliminary report (Czechowski 1990a)]. Pupae from mounds of wood ants were collected by means of wax honeycomb frames (Wiśniewski 1973); their number was estimated by the volumetric method (1 litre = 30,000 pupae). The number of pupae introduced into a nest and the percentage of slaves that emerged in a mixed society provided a basis for determining an approximate

initial abundance of a *F. sanguinea* colony (Table 1) [assuming that there had been some insignificant losses of pupae; see: Czechowski (1989)].²

F. polyctena pupae introduced into a given colony of *F. sanguinea* came (depending on their number) from one or more nests (mainly from the same polycalic colony). They were provided (also depending on their number) in one or several batches, and this ensured that each time there was enough room for them in the nest (see: Czechowski 1989). *F. rufa* pupae came from four monocalic nests and were provided in four (mixed) batches. The *F. sanguinea* colonies were supplied with pupae from the end of June till August, but mainly in July. The percentage of slaves was determined after their entire emergence in autumn (the end of September), then in spring (April–May), summer (July) and autumn of the following year. In order to do this, random samples of ants were collected from the surface of a nest after disturbing the colony a little. Regular observations covered the experimental colonies and the nearby normal colonies of *F. sanguinea* throughout the season.

Apart from this, as a control, one colony of *F. sanguinea* (SF-I) was provided with *F. fusca* L. pupae. These were collected, by means of a vacuum cleaner, from many nests from mid-July to mid-September.

One of the colonies (SP-V) appeared to be a temporary branch of another one (SP-IV); all the pupae provided there were carried by *F. sanguinea* to its main nest. Colonies SP-I, -II, -VIII, and SR-I

² In colonies of amazon ants, eg *Polyergus lucidus* Mayr, most of the pupae captured may be devoured (Cool-Kwait, Topoff 1984). However, in amazon ants, unlike in *F. sanguinea*, foraging is exclusively the duty of slaves and therefore it is no wonder that food may be in short supply. Furthermore, pupae captured by slave-keeping ants themselves come to the nest gradually and in batches smaller than those provided experimentally. Thus, under natural conditions far fewer of them have any chance of undergoing complete metamorphosis. Nevertheless, the values of the initial colony size of *F. sanguinea* obtained on the basis of the percentages of slavers and slaves in ant samples collected from the surface of (slightly disturbed) nests must be treated with great caution – simply as indicative values. Such data could be entirely reliable only on the assumption (out of the question here) that the percentage of the emerged slaves was identical in each of the nests, and that the surface samples represented the proportion of species real for the whole colony.

were situated far from one another. However, Colonies SP-III and SP-VII, and also SP-IV, -VI, -IX, -X and SF-I were very near. The latter were a part of a larger *F. sanguinea* complex. Yet all the colonies formed separate (monocalic) societies. They did not keep in contact and alien workers (confronted experimentally) displayed something of an aggressiveness (dragging) towards one another.

As a result there were 10 mixed colonies in which wood ants were the slaves of *F. sanguinea* (9 nests with *F. polyctena* and one with *F. rufa*). The initial proportions of the slaves were comprised within a large range: from 29% (SP-VIII) to 96% (SP-I) (Table 1). Almost all the *F. sanguinea* colonies studied contained "natural" slaves of the genus *Serviformica*: *F. cunicularia* Latr. and (or) *F. fusca*. Their insignificant proportions of these (only a few per cent) had no bearing on the calculations or the course of the experiments.

RESULTS

Slave emancipation

Emancipation of slaves occurred in all or almost all the SP and SR colonies (only in the case of Colony SP-VIII the fact of emancipation was not recorded most certainly). During the spring of the second year of the experiments the swarms of the social parasite gradually disappeared and *F. sanguinea* queens were replaced by young queens of wood ants adopted after their nuptial flights by orphaned swarms of (former) slaves. The adoption of queens was discovered either directly (SP-I, SR-I) or indirectly, on the basis of the emergence of brood (a new worker generation) of wood ants in (former) nests of *F. sanguinea*. Colonies SP adopted conspecific queens and developed (or, at least, started to develop) into congeneric societies of *F. polyctena*. The oldest (and the biggest) of them, SP-I and SP-II, even began producing their own alate queens (starting from 1990). Colony SR-I simultaneously adopted *F. rufa* queens (conspecific to the ex-slaves) and *F. polyctena* ones, thus becoming a potentially permanent bispecific society (Czechowski 1991b).

As concluded earlier (Czechowski 1990a), the emancipation of slaves was achieved through elimination in some way (killing?) of *F. sanguinea* queens

and devouring their offspring. In colonies with a relatively small percentage of slaves (SP-VIII, -IV, -III) *F. sanguinea* survived a little longer (Table 1), and this may have been due to incomplete annihilation of the new generation of its workers. It must be underlined here that there were recorded absolutely no signs of hostility of slaves (and later ex-slaves) towards adult *F. sanguinea* workers throughout their life together.³ The latter died out naturally. The two presumed mechanisms of emancipation (elimination of the queens and brood of the slavers) were (at least in great part) confirmed when two experimental nests, SP-IX and SP-X, had been dug out. This was done in autumn (7 September, 1990), more than two months after the introduction of *F. polyctena* pupae (18 June into SP-IX; from 18 June to 4 July into SP-X). No queens were found in each of the nests (of course, this can not be regarded as an uncontroversial evidence that the colonies were really queenless, especially if they were monogynous). Only four *F. sanguinea* pupae were found in SP-IX and there was no brood at all in SP-X. Before the introduction of slaves, both colonies had had their own offspring and in September all the nearby untouched nests of *F. sanguinea* were full of their own pupae.

The case of Colony SP-III is puzzling. In 1989, the initial share of slaves there was 52%. In the following spring (1990) *F. polyctena* already constituted 97%, and in autumn 98%. There emerged a new generation of workers – a sign that a queen (queens) had been adopted. Meanwhile, in spring 1991, the share of *F. sanguinea* workers increased to 14%. The difference in the ratios of both species in this sample ($n = 118$) and in the previous one ($n = 60$) is statistically significant (d -test; $P = 0.01$). Therefore, readoption of a *F. sanguinea* queen cannot be ruled out. Maybe, she had survived in the vicinity of the nest, together with a group of her own workers which still were in some contact with the rest of the mixed colony. Since something of the kind of bispecific oligocalic colonies of *F. sanguinea* + *F. rufa* (Marikovskiy 1963) and of *Polyergus rufescens* (Latr.) + *F. cinerea* Mayr (Czechowski 1975b) which function on the principle of oligogyny are possible, it follows that a monocalic oligogynous colony of this

³ In species of the genus *Camponotus* Mayr the adopted alien brood kill the host workers (Carlin 1988).

type is also conceivable (although it seems rather unlikely). Forel (1874, 1928), too, recorded cases of mixed colonies of *F. sanguinea* + *F. pratensis* surviving for several years without any intake of new slave pupae. He ascribed this to a very long life span of workers observed under laboratory conditions. However, potential longevity and real longevity under field conditions are two different things (Dobrzańska, Dobrzański, pers. comm.). *F. sanguinea* workers in the Gorce Mts lived for 20–22 months at most (this included two winters).

No emancipation of slaves was recorded in Nest SF-I (with *F. fusca*). This experiment, regardless of its result, must be considered a failure. The *F. sanguinea* swarm consisted of no more than 5,000 workers and the naturally enslaved *F. fusca* individuals constituted 5% of the colony. In spite of the fact that 20,000 pupae were provided, the share of *F. fusca* increased only to 36%. Thus the losses must have been very high, and this was due to several causes. It was difficult to collect such a great number of *F. fusca* pupae and therefore they were provided over a long period (nearly two months) in many (19) small (100–3,000 individuals) batches. Frequently, the pupae were young and required a long time to emerge. About half of the total number consisted of nude pupae (without cocoons), which were easily damaged during handling. Thus, *F. sanguinea* had a possibility to eat more of these than of pupae of wood ants that were practically at the same age, advanced in their development, always cocooned and provided in “shock” batches.

Nest relocations

In summer, soon after the beginning of the mass emergence of slaves, the mixed colonies changed their place of nesting or at least tried to do so. Only Colonies SP-IV and SR-I had given up their attempts (building initiatory nests) to find new nesting place and remained in their old ones (considerably enlarged and rebuilt). Colony SP-II moved the farthest (25 m) (Czechowski 1990a).

The initiative to move or, more precisely speaking (considering their later attitude), to found new filial nests, generally came from *F. sanguinea* workers. Only later (a removal usually lasted for some weeks) did great numbers of older slaves join the operation. This decided the removal of the entire

colony. Towards the end of the whole operation *F. sanguinea* revealed their conservative attitude. They showed a tendency to remain in the deserted nest, to return to it or they even tried to change the direction of the move. A spectacular attempt at forcing the swarm (still a mixed one) to return to its former nest was undertaken by *F. sanguinea* from Colony SP-VI after the emancipation of the slaves (during the following year, after the introduction of pupae and removal to a new nest). Although they were in minority (8% of the colony), the ex-slavers began, in June, a desperate transportation of the ex-slaves to their old nest (2.5 m away). As a result of this, both nests were inhabited for some time until, in July, *F. polystena* undertook a firm counteraction that sealed the fate of the old nest, which was abandoned altogether.

Nest conservatism in *F. sanguinea* is illustrated perfectly by the case of Colony SP-X. It had changed places three times after the emergence of slaves and before it was dug out. On the day it was dug out the colony inhabited four nests, though to various degrees: the original nest of *F. sanguinea* (A) and the successively changed new nests (B, C, D). The distances between them were 6.5, 3.0 and 3.4 m, respectively. All four were dug out and samples of ants were collected. Nest A was almost completely deserted – only 23 individuals were found there: 1 *F. polystena* (4%) and 22 *F. sanguinea* (96%). Nest B, too, was almost entirely empty – 25 individuals (nearly all) were caught: 8 *F. polystena* (32%) and 17 *F. sanguinea* (68%). Nests C and D were fully inhabited and joined by a route of intensive two-way traffic. In the samples taken from both nests ($n = 59$ and 87) the ratio of *F. polystena* and *F. sanguinea* was identical – 91% : 9% (Fig. 1). The difference in

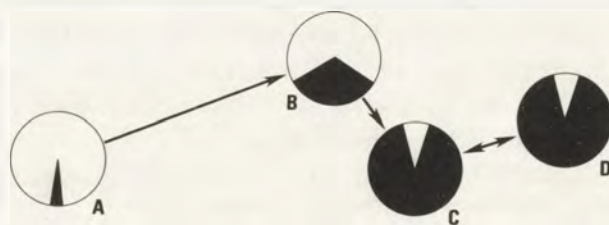


Fig. 1. Nest conservatism of *F. sanguinea* and changes in the proportion of the slavers (white) to the slaves (black) in the successively settled nests of the mixed Colony SP-X.

the proportions is manifest. "Natural" slaves (*F. fusca*), constituting 2% of the mixed colony, occurred only in Nests C and D.

The situation was similar during removals of other colonies, eg SP-III (this, exceptionally, was inspired by the slaves). After nearly a month-long removal the old nest contained 19 ants: 5 *F. polyctena* (26%) and 14 *F. sanguinea* (74%). In the new nest this ratio was 52% : 48% ($n = 81$). The difference is statistically significant (d -test; $P < 0.05$). In this case, too, all "natural" slaves (*F. cunicularia*), constituting 10% of the mixed colony, moved to the new nest.

During an attempted but unrealized removal of Colony SP-VII the ratio of *F. polyctena* to *F. sanguinea* was 73% : 27% ($n = 41$) in the initiatory nest whereas it was 88% : 12% ($n = 108$) in the main one. The difference is significant ($P < 0.05$).

In the light of these facts it can be concluded that *F. sanguinea*, while undertaking the removals, did not intend to change the place of nesting but wanted to found filial nests, probably foraging stations.⁴ As soon as the colony size was suddenly and considerably increased, the ants undoubtedly began to experience a shortage of food. The nests of *F. sanguinea* were situated in more or less open places where their carbohydrate food (honeydew) came from small and dispersed colonies of aphids on herbaceous plants and on small spruces; this was not sufficient in the new situation. The slavers (because their slaves were still too young to forage) were faced with the necessity to provide the greatly increased food requirements of the societies. While expanding the range of foraging they came across rich sources of honeydew in the canopies of old spruces. As a rule, the new nests (stations?) were founded on the edge of a forest or under bigger trees. These new localities were also better than the previous ones as nesting places for wood ants (shade, abundance of suitable building material, a rich source of food close by). No wonder they were preferred by the slaves who were gaining quantitative advantage.

During all the observed removals adult workers and pupae were transported. There were no instances of carrying larvae (and queens), that is offspring,

which could be ascribed beyond doubt to *F. sanguinea* (and larvae of this species should have been present at that time). It is, therefore, evident that the brood of the slave-keepers were destroyed (eaten) very early – at the beginning of a mass emergence of slaves and before establishing new ways of foraging.

A certain (small) number of *F. sanguinea* workers usually wintered in their deserted old nest. These joined the rest of the society in spring (eg SP-VI) or, if they had lost contact, died there in isolation (eg SP-II; Czechowski 1990a).

In one respect the slavers managed to impose their nesting habit on the slaves. In all the cases when *F. sanguinea* had a separate winter nest (SP-I, -II, -IV, -VIII) the mixed colony, or at least a part of it (SP-II; Czechowski 1990a) just wintered there even when their new nest (SP-I, -II) or that greatly enlarged rebuilt one (SP-IV) showed all the signs of all-the-year-round nest of wood ants.⁵ Only in the case of Colony SP-VIII still dominated by *F. sanguinea* (Table 1), did this seem justified. But even the four-per-cent minority in SP-I forced an autumn removal of the entire colony to their winter nest which had been left unused throughout the season. What is more, this nest had to be rebuilt very quickly because its mound had been pulled down and the material used for the new nest (Czechowski 1989).

Nest conservatism of *F. sanguinea*, recorded during the experiments, may have been the cause of the phenomena described by Marikovskiy (1963) – the separation of swarms of the parasite and its victim. As a result of such an interpretation the difference in the gist of the phenomena recorded in the Gorce Mts and in Western Siberia becomes invalid, the latter phenomenon being reduced to special instances of the former. If *F. sanguinea* queens had been eliminated during the time when both species were living together, their readoption could have been provided a possible difference (overlooked, maybe, by Marikovskiy).

⁴ It cannot be ruled out, however, that these were emancipation attempts made by... *F. sanguinea*.

⁵ Wood ants colonized artificially during late summer (or even in autumn; Czechowski, unpubl. data) in non-optimum habitats are able to prepare nests that ensure safe overwintering (Pisarski, Czechowski 1990).

Relations with other colonies

Among all the experimental nests, only SP-III and SP-VII were situated close enough (9 m) to make direct contact of the foreign colonies possible. Each of them occupied a heap of stones that had been formed on a grassy slope. The heaps were old, overgrown with thermophilous vegetation (dog-rose, raspberry and blackberry bushes, wild strawberries, and thyme) – typical habitats of *F. sanguinea*. The colonies had made no contacts before *F. polyctena* were introduced. Individuals experimentally relocated for control reasons were recognized as foreign (they made the local ones interested and agitated) but provoked no distinct aggressiveness.

During the first year of the experiment, in mid-September of 1989, Colony SP-VII built a small initiatory nest in a stretch of grass dividing the sites of the two nests. In this way the ants came closer (6 m) to an old, still partly inhabited nest of Colony SP-III. This colony immediately reacted to a change in the status quo. A loose column of excited workers started out towards the new nest, stopped 0.5 m before their target and formed a restless concentration – as during an ordinary raid of *F. sanguinea* (Czechowski 1975a, 1977). *F. sanguinea* were the main participants of this operation although Colony SP-III was (slightly) dominated by *F. polyctena* then. No attack followed. The operation looked like a warning given to a (known) neighbour who was trespassing against the established norms of coexistence. On the following day the initiatory nest of Colony SP-VII was completely deserted.

On the one hand, this incident pointed out to some connection (genetic?) between both colonies of *F. sanguinea* (which refrained from open aggression) but on the other hand, it stressed their current separateness. The latter acquired special importance in the light of a later event. Now, both these colonies – of already emancipated slaves but still with some *F. sanguinea* (Table 1) – fused at the end of June of the following year. The fusion automatically included the remainders of both slave-keeper swarms. The union was initiated by *F. polyctena* from SP-VII who had first made contact with their conspecifics from SP-III and then moved to their (new) nest situated 12 m away from Nest SP-VII.

The relations of the mixed experimental colonies with foreign untouched *F. sanguinea* colonies were completely different. The latter attacked the former and treated them as sources of slaves for themselves. Such attacks were directed at Colonies SP-VI (twice) and SP-VIII. The first attack on SP-VI took place one month after the colony had been provided with pupae, at the beginning of mass emergence of *F. polyctena*. The course of the conflict was very interesting and the whole affair was a failure and the aggressor withdrew (see: Czechowski 1990b).

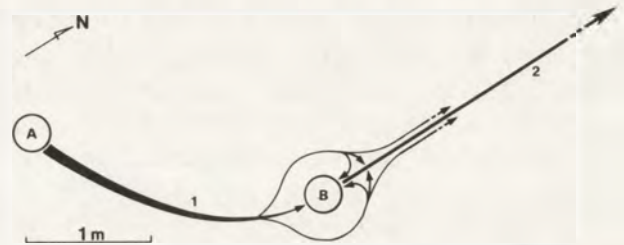


Fig. 2. Aggression of *F. sanguinea* (N-II) towards the mixed Colony SP-VI: A – old nest of SP-VI, now occupied by Colony N-II; B – new nest of SP-VI; C – old temporary nest of Colony N-III of *F. sanguinea* (see: Czechowski 1990b), now a shelter for a part of the ants from SP-VI; 1 – raid of *F. sanguinea*: direction of the attack, manoeuvre and chase; 2 – direction of the escape of Colony SP-VI.

Colony SP-VI was attacked for the second time in the following year (1990), after slave emancipation. As had happened before, the alien *F. sanguinea* (N-II) first settled (at the end of July) in the near vicinity – this time occupying a deserted old nest of Colony SP-VI (Fig. 2).⁶ The aggressor attacked on 3 August, in the morning, and outflanked Nest SP-VI on both sides. The attacked ants defended their colony at the base and then on the mound surface. In the course of this, their evacuation route was quickly revealed and it led directly to a place 24 m away – far beyond the regular range of the colony. At first, pupae were transported only sporadically. Then, at noon, a big group of *F. polyctena* (together with the remainders of *F. sanguinea*) suddenly returned from the place of evacuation to the attacked nest and initiated a mass flight with their pupae. Among those transported this time there were ob-

⁶ Colonies of *F. sanguinea* move from one place to another in search of prey (Rosengren et al. 1986).

served some big pupae which turned out to be pupae of *F. sanguinea* males(!), which means the offspring of orphaned workers. (And they were being rescued by *F. polyctena* workers!). [Some *F. sanguinea* workers may have well developed ovaries (Möglich, Hölldobler 1974), however male production by workers was not reported earlier in this species]. A moment later the aggressors completely encircled the nest and intercepted the rest of the evacuation column. The ants that had managed to break through were chased for over 5 m and their pupae were taken away. The whole of Nest SP-VI was captured. Colony N-II managed to seize two-three thousand pupae; most had been taken away in time. After the combat from an area of 800 cm² at the mound base of Nest SP-VI dead ants were collected: 75 (66%) *F. polyctena* and 39 (34%) *F. sanguinea*. The total number of casualties was not much higher.

In its new place Colony SP-VI made a bivouac in a tuft of grass and the ants stayed there passively for three rainy days. When the weather improved they immediately begun searching for their nestmates, dispersed during the conflict around, their (old) nest. A large group (with pupae) had gathered under a stone 3 m away from the nest (in a deserted temporary shelter of the previous year's aggressor; Czechowski 1990b). The rescue operation was very competent. There was no doubt that it had been undertaken with just this intention. The ants that were involved in it picked their way among numerous foreign *F. sanguinea* individuals penetrating the area – but these were ignored by the searchers interested only in finding their lost nestmates.

Colony SP-VI (additionally supplied with *F. polyctena* pupae) built a new nest, far from the old one which had been taken over by the aggressors for good. Colony N-II retained its species status; the number of *F. polyctena* pupae captured must have been insufficient for emancipation of the slaves. An inspection carried out in September 1991 revealed no presence of *F. polyctena* in Colony N-II.

Colony SP-VIII was attacked by *F. sanguinea* nesting about 20 m away. This occurred at the end of July 1990 when *F. sanguinea* workers were still quite numerous in the colony (Table 1). The raid was not recorded but its results were evident: Nest SP-VIII was occupied by alien *F. sanguinea* (and functioned as its branch till the end of the season) and

there was no trace of the experimental colony. In autumn, however, there were recorded no *F. polyctena* workers (emerged from allegedly captured pupae) in the nest of the aggressor. But the foreign colony of *F. sanguinea* was very large whereas pupae in SP-VIII were very few (species affiliation of the latter had not been checked). It is also possible that the attacked ants managed to escape without great losses and they later built a new nest somewhere else.

An unusual form of kidnapping (eudulosis) was employed by *F. sanguinea* towards Colony SR-I at the turn of August and September 1990. That colony was after the emancipation of a slave swarm of *F. rufa*, already a mixed one – *F. rufa* + *F. polyctena* (see: Czechowski 1991b). Its age structure was not typical either – the old *F. rufa* workers (ex-slaves), very few all along, were already dying out and the new, very numerous mixed generation (the first offspring of young queens) was only beginning to emerge. Thus the majority of the colony consisted of very young and weak workers which were forced, too early, to undertake tasks outside the nest. Some *F. sanguinea* workers (from an unidentified colony) wandered singly round the nest and captured these callow ants (without doing them any harm). However, it is possible that, in the autumn, Colony SR-I was openly attacked because by the following spring its nest was deserted. But the colony had tried to change its nesting place earlier because of the tiresome presence of a strong *Lasius niger* (L.) colony, manifesting an aggressive attitude.

The relations between *F. polyctena* ants from the experimental and natural colonies depended on the current status of the former. They were definitely hostile during the first year of the experiment (Czechowski 1989, 1990a) but normalized after slave emancipation. For instance, between the initially (1987) hostile Colonies K-III (natural) and SP-I, during the second year (1988) there was formed a “no ants zone” (Czechowski 1990a); later on (1989–1990) a border impassable for both parties; then (1991) the colonies formed a federation – SP-I moved into the territory of the stronger partner but kept its individual character; finally (1992), Colony SP-I moved into one of the two, at that time existing, nests of K-III, probably because its own nesting place had become too overshadowed. This “re-

straint" in developing comity should be associated not so much with the origin of the ex-slave colony but more with the time of its appearance within the range of Colony K-III. Artificially founded colonies of *F. polyctena*, even of different origin, show a strong tendency to merge when they are colonized during the same year. However, already stabilized colonies (for instance, established the previous season) tend to preserve their separateness in relations with younger ones, even of the same origin, and their initial contacts are more or less aggressive (Pisarski, Czechowski 1990, Czechowski, unpubl. data). The case discussed here, when Colony SP-I (already independent) appeared near K-III (a resident of the area), may be considered a special case of artificial colonization (which, in fact, it was; Czechowski 1991a).

As mentioned above, new "artificial" colonies merge without any problems during the first year of their existence; just like worker groups under stress. When Colony SP-VI, weakened after its conflict with alien *F. sanguinea*, was staying in its bivouac the ants were provided with *F. polyctena* pupae taken from the same polycalic colony from which pupae for *F. sanguinea* had been collected a year earlier. There were about 10,000 pupae together with several hundred workers and some nest material. Not the slightest conflict between the ex-slaves and the new *F. polyctena* ants was recorded. The strewn pupae were carried into the bivouac by all of them side by side. But SP-VI still contained some *F. sanguinea* workers. They joined the crowd of alien *F. polyctena* perfectly trustfully, without the least hesitation or any signs of hostility and they tried to collect some pupae. However, the newcomers recognized them immediately, attacked fiercely – and killed all of them!

DISCUSSION

The ability to distinguish between nestmates and non-nestmates within the species and the ability to recognize foreign species are the basic element of the social organization in insects. Both depend, first of all, on colony-specific chemical signals (and species-specific on the species level). There still is a lot of ambiguity and controversy

concerning the origin, sources and biochemical nature of these signals (Hölldobler, Michener 1980, Sudd, Franks 1987, Hölldobler, Wilson 1990). The most recent discoveries point out to surface pheromones, particularly to cuticular hydrocarbons (CHC), as the probable olfactory discriminators (or the so-called colony labels) in various groups of social insects, including ants (Bonavita-Cougourdan, Clément 1986, Bonavita-Cougourdan *et al.* 1986, 1988, Yamaoka *et al.* 1988, 1990, 1991). The composition of the CHC mixture is species-specific and genetically controlled. However, as any other character, this is also subject to individual variability. This variability for a given colony falls within the range of the species variability and is the resultant of the odour variability of all the members of a given society. Individual odours are standardized (mixed) in the course of intracolony inter-specific social contacts (Yamaoka 1990, 1991). The role of the queen is still controversial: is she the main source of the identifier of her colony (Carlin, Hölldobler 1983) or is her impact in this respect reduced to her role as the centre of social life in which the odour is standardized (Yamaoka 1990)?

The ability to recognize nestmates (and the attitude towards non-nestmates) is decided by the early experience of workers imprinting the odour stimulus from the social environment of the callow ants (Jaisson 1975, 1980, Jaisson, Fresneau 1978, Le Moli, Passetti 1977, 1978, Le Moli, Mori 1982, 1984). All kinds of mixed societies, including slavers and their slaves, are excellent for studying these phenomena (nestmate-, kin- and species recognition, acquisition and mixing of odours, stability of imprinting and the odour acquired). It is just the plasticity of callow ants that makes dulotic species successful (Le Moli 1980, Le Moli, Mori 1985). However, it is not only this. The extremely specialized slavers, ie amazon ants (eg *Polyergus samurai* Yano), do not synthesize their own species-specific CHC but they obtain them extemporaneously from the slaves they have at a given time (Yamaoka 1990).

Has *F. sanguinea* a possibility of such chemical mimicry? It seems that even it so, this possibility is limited. This is shown by the fate of the (ex-)slavers which, after a year among a swarm of *F. polyctena* (SP-VI), were easily recognized and destroyed by

some other *F. polyctena*. It must be pointed out here that the *F. sanguinea* individuals that had survived until then were, most probably, the remainder of a new generation which had not been eaten completely by the slaves. Therefore they emerged among the swarm of *F. polyctena* and as callow ants they were (theoretically) particularly liable to acquiring a foreign odour. However, their own species-specific label appeared to be impossible to hide even in such an extreme situation. (Though it would be interesting to know how ants of typical slave species would have behaved if they had been there instead of *F. polyctena*). Bergström and Löfquist (1968) have found evidence of odour similarity between *F. sanguinea* and some *Serviformica* species but this general similarity may be a phylogenetic achievement of the social parasite and thus an innate character of the species. Moreover, these slave-keepers, quite unlike amazon ants, frequently live without slaves. And it is difficult to imagine a colony functioning without any discriminator.

Slaves treat the nest of their slavers as their own. This statement is a truism if it refers to the ants *Serviformica* whose biology generally predestines them to play the role of victims of social parasitism (eg dependent founding of nests by *Formica* s. str. or *Coptoformica* Müll. queens). The fact that the mechanisms of chemical "indoctrination" work also on wood ants emphasizes the power of their impact. Normally, wood ants and *F. sanguinea* seem to be the most fiercely fighting opponents in the entire Palaearctic myrmecofauna. The same is emphasized also by Marikovsky (1963).

The phenomenon of slave emancipation described here raises some doubts in matters that have already seemed explained. First the question arises: why the slaves, while approving of adult *F. sanguinea* workers, destroyed the brood of the latter. According to Jaisson's suggestion (pers. comm.) the possible cause lies in the quantitative disproportion between the artificially introduced slave pupae and the offspring of the slavers. It follows from this interpretation that the slave callow ants (liable to imprinting) that were emerging in great masses were mainly surrounded by a crowd of their conspecifics. During their early education they had not much chance of getting in contact with a larva or a pupa of the proper host of the nest. As a result, in

their adult life, they recognized *F. sanguinea* brood as foreign.

This hypothesis has weak points. First, everything took place inside natural nests of *F. sanguinea*, saturated with their specific odour, and under conditions of great overcrowding. Second, the slaves manifested no aggressiveness towards adult workers of the slavers which, too, frequently occurred in proportionally insignificant numbers (eg SP-I, -II, -VI, -IX, -X). And, after all, it is a rule in social Hymenoptera that alien brood is accepted more readily than adults (Hölldobler 1977, Hölldobler, Michener 1980, Carlin 1988). (The last argument, however, may be undermined by drawing attention to the activity of *F. sanguinea* workers in their contacts with young slaves – they help them during emergence, feed them etc., and this means that their mutual contacts are intensive). Third, the slaver brood was eliminated even in those cases when the percentage of slaves was not so high. Fourth, it did happen that, already after emancipation and in nearly monospecific colonies of *F. polyctena*, the remaining *F. sanguinea* workers managed to have their own offspring (males) which were looked after by *F. polyctena* (SP-VI). Fifth, what about slaver queens? They, too, somehow fell a victim to the slaves.

Yet another explanation, though not fully satisfactory either, may be suggested. Now, as soon as the abundance of the colonies increased rapidly the ants were short of food. Hunger forced them to eat their brood; this occurs frequently in ants (Wilson 1971). In an earlier paper (Czechowski 1990a) an assumption was put forward that each of the species – members of a given mixed colony selectively had devoured the brood of the other and this had put *F. sanguinea*, less abundant by far, in a hopeless position. However, it has been discovered now that the offspring of the slavers disappeared even when the slaves were in a minority. Therefore, there remains an alternative explanation determined by the economics of a mixed society as a whole: the younger brood were eaten. And, accordingly to the difference in the phenology of the two species, the brood of *F. sanguinea* were younger.

Even this hypothesis, however, does not explain the causes and circumstances of the *F. sanguinea* queen elimination. It is possible that it was slaver

queens who were intolerant (aggressive) of atypical slaves and were killed by the latter in self-defence(?).

If, on the other hand, the reason for the elimination of the *F. sanguinea* brood was other than hunger then the question is whether this phenomenon was conditioned by the number (relative or absolute) of the slaves. Was, thus, the elimination of queens conditioned as well? And what is this possible minimum number (or percentage) of slaves (from the point of view of *F. sanguinea*, the crucial permissible minimum)? The experiments have shown that both phenomena occur already when the proportion of (atypical) slaves is about 50%. Does this not mean that wood ants (as species) have at their disposal a peculiar safeguard against social parasitism practised by *F. sanguinea*, and this makes the latter helpless against it?

And another question still remains open: are typical slaves, ie the *Serviformica* species, capable (even if only potentially) of do likewise?

The last matter concerns the permanence of imprinting and an individual's own and acquired odour discriminator. At the beginning of their life in a mixed colony, highly dominated by slaves, these very slaves – at the side of the relatively few slavers – fought against their own conspecifics (even former nestmates) and the latter considered the former to be their enemies (SP-I, -II). The mechanism of this is well-known: on the one hand, imprinting of the odour of the slaver colony instead of their own colony- or species-specific label, and on the other, a camouflaging effect of this acquired odour against the inherited discriminator. However, after a year (SP-VI), the same individuals (the new generation was to emerge later on) were friendly towards their conspecifics and were treated likewise in return. This means that the original imprinting (from the callow period) had died out and the influence of the foreign odour was gone too (the latter is easy to understand because of a change of nest and a minimized share of the former slavers). However, contrary to what might have been expected the relations between *F. polyctena* and *F. sanguinea* after slave emancipation did not undergo a symmetric reversal. The last ex-slavers remaining for a year in the nest of the ex-slaves (and quantitatively dominated by them even more than at the beginning) did

not recognize alien *F. polyctena* as an enemy, but they themselves were perceived as such (SP-VI). The camouflaging effect of another's discriminator proved ineffective in this case.

In other words: in a colony of *F. sanguinea*, *F. polyctena* became, until its emancipation, «sanguinea» – in its own “feeling” and for the alien *F. polyctena*. After emancipation it again “became itself” – for itself and for others. On the other hand, *F. sanguinea* after the emancipation of its slaves became «polyctena» but only in its own “feeling”. Why? Was this due to some kind of the influence of the presence (or absence) of foreign (and their own) queens?

Some of the above questions may be explained if the experiments are repeated under laboratory conditions. Others require precise biochemical studies. Let these speculations be finished with a reminder of August Forel's experiment, of last century, in which both the very idea and the result were amazing. (Forel repeated the experiment in many variants with the same effect). He shoved *F. sanguinea* and *F. pratensis* colonies into one bag, tied the bag up, shook it vigorously and left for a few days. It turned out that, after an initial massacre, the colonies fused into one mixed society which remained in this form after the ants had been released (Forel 1874, 1928).

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