POLISH ACADEMY OF SCIENCES ★ INSTITUTE OF ZOOLOGY
MEMORABILIA ZOOLOGICA

MEMORABILIA ZOOL.	44	55–63	1990

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Autonomization of slaves from mixed colonies of *Formica sanguinea* LATR. & *F. polyctena* FOERST. (*Hymenoptera, Formicidae*)

Abstract. Two colonies of *Formica sanguinea* LATR. were artificially supplied with great numbers (230,000 & 250,000) of pupae of *F. polyctena* FOERST. This was the beginning of mixed colonies with enormous predominance of atypical slaves (96% & 80%). The mixed swarms lived without conflicts during the year they were formed. During the spring of the following year *F. sanguinea* disapperared from them altogether, ex-slaves adopted conspecific queens and the colonies, originally of *F. sanguinea*, were transformed into pure colonies of *F. polyctena*. The experiments were made in the Gorce Mts. (Western Carpathians) in the years 1987–1989.

INTRODUCTION

A previous paper (CZECHOWSKI 1989) presented the origin, development and functioning (division of labour) of a mixed colony of *Formica sanguinea* LATR. and *F. polyctena* FOERST. (SP-I; a symbol given now), and also its relations with a nearby (artificially established) colony of *F. polyctena* (K-III). The experiment was carried out at Ochotnica Górna in the Gorce Mts. (Western Carpathians, the Western Beskidy Mts., southern Poland) in 1987. Observations were discontinued in mid-September that year. The mixed swarm, in 96% consisting of atypical slaves, inhabited a newly built summer nest. Its previous summer nest had been abandoned and partly demolished; the winter nest, left for the season, had also been partly demolished. The contacts (hostile) between Colonies SP-I and K-III came to an end.

DESCRIPTION OF THE OBSERVATIONS AND EXPERIMENTS

Autonomization of slaves

After the winter interval the observations were resumed in mid-May and the following state of affairs was recorded. The sumer nest of Colony SP-I, that had been inhabited the previous autumn, did not exist any longer; it had been completely demolished. Material thus obtained had probably been used for the reconstruction and expansion of the winter nest which dimensions were much bigger (∅ = 30/40 cm, h = 25 cm) and where the ants had overwintered. In mid-May they were just beginning to settle in their summer nest that was being developed (its dimensions at that time were: ∅ = 40/45 cm, h = 5 cm). It rained from 20–23 May and

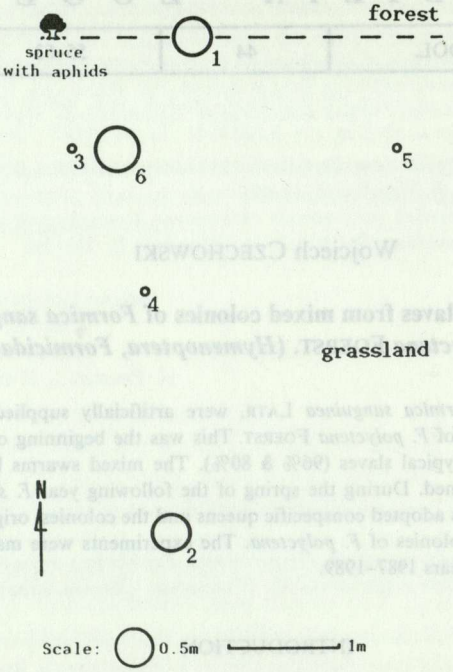

Fig. 1. Distribution of the nests of Colony SP-I: 1 – winter nest; 2 – summer nest; 3–5 – temporary initiatory nests; 6 – new permanent nest.

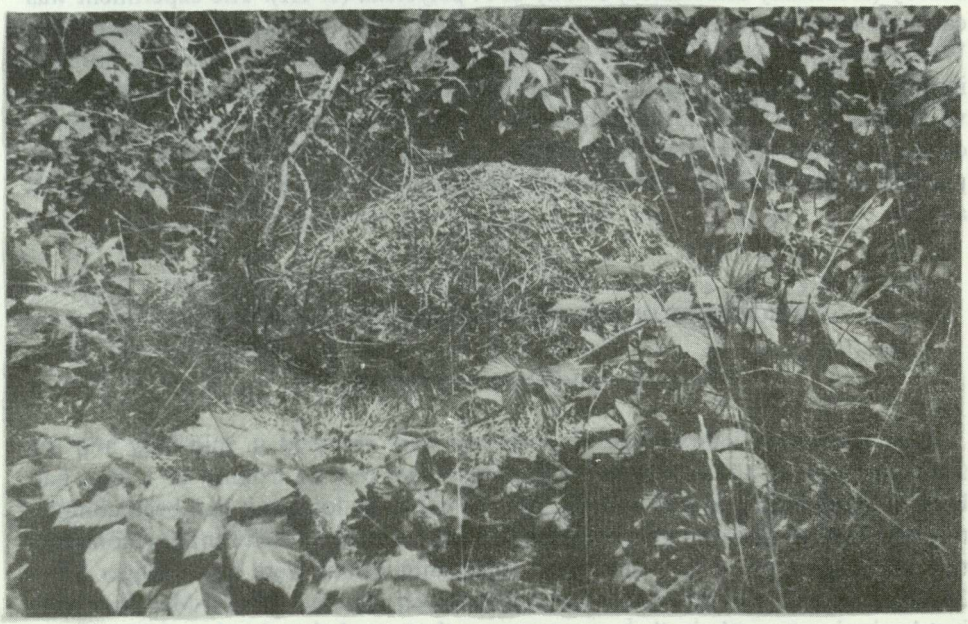

Fig. 2. Nest od Colony SP-1 in 1988 (Photo by W. CZECHOWSKI).

just then the two nests (both the winter and the summer one) were destroyed by a woodpecker. As a result of this the ants abandoned them and built four initiatory nests in the neighbourhood. One of these became a permanent nest in mid-June (Fig. 1).

At the end of May it was recorded that Colony SP-I (very vital one) consisted entirely of *F. polyctena* workers. *F. sanguinea* had disappeared without trace! On 25 May many (up to 10 at a time) wingless queens of *F. polyctena* were spotted near the newly built summer nest. They either were being carried by workers or moved among them freely. No doubt, they were young fertilized queens just adopted after their nuptial flight. [The nearest colony of *F. polyctena* producing alate queens was Colony K-III situated next to SP-I; the nearest colony producing males (J–XXIII) was 1.5 km away]. Colony SP-I soon had its own offspring. The first larvae (worker ones) were recorded on 1 July. Towards the end of the 1988 season the mound of the nest (built from the very beginning during that year) reached the dimensions: ∅ = 65 cm, h = 35 cm (Fig. 2). At present (1989) this colony – originally of *F. sanguinea*, later a mixed one – functions as a normal, independent colony of *F. polyctena*.

Any possibility that the swarm of *F. sanguinea* had moved out and settled in a different place was ruled out. The habitat suitable for this species was small and the whole area was searched very carefully. On the other hand, there were no indications that *F. sanguinea* workers had been physically exterminated by the slaves. It was quite probable that the experiment had been conducted on an orphaned (queenless) swarm of *F. sanguinea* that had been dying out in a natural way. [That was the last living colony of a now regressing but originally polycalic society (CZECHOWSKI 1989)]. For this reason the experiment was repeated in 1988.

The new target was a colony of *F. sanguinea*, SP-II, situated about 50 m from SP-I. This, too, was a monocalic colony but, no doubt, a developing one. It had not only its main summer nest but a few small accessory ones as well. The main nest, with the soil mound that dimensions were: ∅ = 30 cm, h = 10 cm, was placed among the grass on the top of a stony slope near a road. The accessory nests were situated on the slope, under stones. The winter nest (empty that time), at 9 m from the summer one, was hidden among bushes on the edge of a forest (Fig. 3). The colony produced offspring, including larvae of sexuals. It had a small number of *F. fusca* L. slaves.

Table. The course of enriching Colony SP-II with pupae of *F. polyctena*

Date	Number of sets of wax bee combs	Number of pupae	Nest of origin of pupae
29 June	5	60,000	S-XIII, S-XV, J-VIII, J-XXIII
4 July	5	65,000	S-IA, S-IV, S-VI, S-XIII
9 July	2	15,000	S-I, S-VIII
17 July	5	85,000	S-IX, S-XI, S-XIV
26 July	2	25,000	S-IV, S-X
Whole period	19	250,000	Colonies S & J (13 nests)

From 29 June to 26 July, Colony SP-II was supplied with about 250,000 of *F. polyctena* pupae, given in 5 batches, that were delivered by means of a method described elsewhere (CZECHOWSKI 1989). The majority of the pupae were taken from a polycalic colony S (Table) – the same which had provided pupae for the experiment with Colony SP-I. The first visible sign that such a huge numer of pupae had been accepted was the fact that the mound of Nest SP-II was expanded in size several times. At the end of July its dimensions were: ∅ = 120/60 cm, h = 15 cm. But as early as 7 July an initiatory branch was being built at 22 m from the main nest. It was situated at the foot of the slope, 3 m below the edge of a beech-spruce-fir forest (Fig. 3). The building of the branch was initiated by *F. sanguinea* that transported great numbers of workers and pupae of *F. polyctena* to the new place. Older slaves also took active part in the removal, but a little later. In mid-July the branch reached a diameter of 30 cm and was abandoned, but the ants built a new branch nearby (about 1.5 m away) and this soon served as a foraging station. It lasted, keeping this function, until the end of August, and reached a diameter of 50 cm. Another branch was begun in mid-August and this was situated 4 m from the station (about 25 m from the main nest). At the end of August its dimensions were: ∅ = 65 cm, h = 35 cm and this became a new main nest. The previous one had been almost completely deserted – only few *F. sanguinea* workers remained there.

There seem to be two reasons for a change in the nesting place of the mixed swarm. The first permanent (summer) nest was in an open area, among herbaceous vegetation, and the ants had no possibility to expand it to meet the requirements of a rapidly growing swarm (lack of building material). At the same time, there were no constant and rich sources of food near the nest. The removal eliminated both drawbacks. The new place guaranteed an excess of building material (mainly the husks of beech buds) and plenty of honeydew on spruce trees (the main source of carbohydrate food was found on a spruce tree growing merely 2.5 m from the new nest) (Fig. 3).

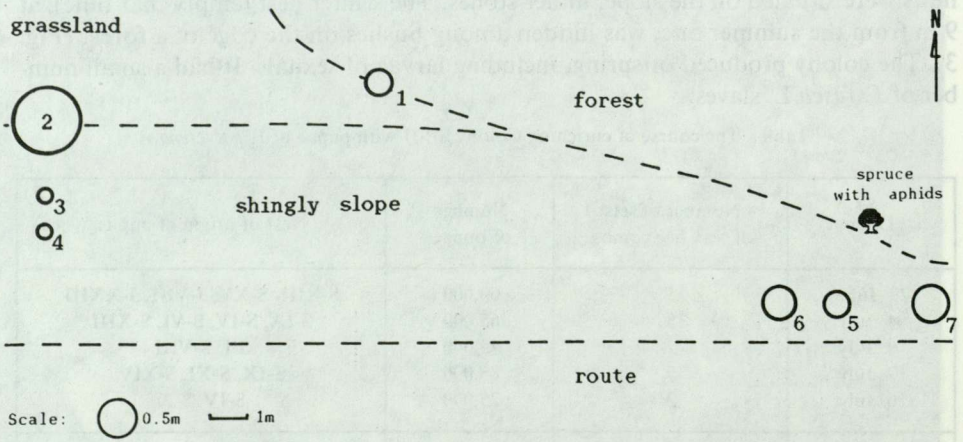

Fig. 3. Distribution of the nests of Colony SP-II: 1 – winter nest; 2 – summer nest; 3, 4 – accessory nests; 5, 6 – temporary initiatory nests; 7 – new permanent nest.

The composition of Swarm SP-II was checked on 1 September (5 weeks after the last batch of pupae had been delivered). Out of the 109 individuals collected at random from the (alarmed) colony 22 ants (20%) belonged to *F. sanguinea* and 87 (80%) to *F. polyctena*. Thus, even assuming that about one-fifth of the pupae supplied may have been used as food in the colony, the initial abundance of the *F. sanguinea* swarm was estimated as reaching at least 50,000, and that was a lot.

The 1988 observations were terminated at the end of September and in the following year they were resumed on 7 April. Colony SP-II was already very active and ants inhabiting the main nest were busy fetching workers that had overwintered in the vicinity, under roots of trees. A great number of workers that had overwintered in the old winter nest of of *F. sanguinea*, 16 m away, returned during the first two weeks of May (Fig. 3). A random sample of 157 individuals was collected from the colony on 12 April; *F. polyctena* constituted 100% of the sample (!). However, a few (ex-)hosts of the nest could be spotted in the colony among masses of (ex-)slaves. Several *F. sanguinea* workers survived in the summer nest that had been almost completely deserted during the previous season. But by the end of June *F. sanguinea* had disappearead altogether. Colony SP-II, just as SP-I in the previous year, began its life as a fully independent society of *F. polyctena*. At the end of September 1989, when the observations were finished, the nest had the following dimensions: $\varnothing = 70$ cm, $h = 40$ cm, and it was fully saturated with ants (Fig. 4).

Fig. 4. Nest of Colony SP-II in 1989 (Photo by W. CZECHOWSKI).

Relations with other *F. polyctena*

The relations of the mixed colony SP-I prior to the autonomization of slaves with other conspecific ants (Colony K-III) have been described in a precious paper (CZECHOWSKI 1989). They were expliciply hostile. The situation was the same in the case of Colony SP-II. On 1 September, a branch of *F. polyctena* was artificially established at 20 m from this nest. The branch had been taken from Colony S, maternal for most of the slaves from the mixed colony. It took Colony SP-II only 3 hours to slaughter nearly the whole, about 20,000 individuals strong, branch. The attack was made almost exclusively by the slave individuals of *F. polyctena.*

The situation changed when the swarm of slaves got rid of the social parasite, but did not happen all at once. Throughout the 1988 season the natural borders of the penetration ranges of Colonies SP-I and K-III never touched. Therefore there were no spontaneous contacts between alien ants. Separate individuals, however, that were experimentally transferred from Nest K-III to SP-I (and vice versa) at first were attacked (in spring) but later were accepted (in late summer and in autumn). Similar changes with time were recorded in the relation of Colony SP-I (but not of K-III) towards small branches of *F. polyctena* that were artificially built in the neighbourhood. Such microcolonies (several thousand individuals strong) were established several times during the season (from the end of May to the beginning of September), generally in the narrow belt between the territories of Colonies SP-I and K-III. This position guaranteed that the scattering ants would come into contact with both neighbours at the same time. Most of the artificial branches came from the polycalic colony S that was maternal for the ex-slave swarm SP-I.

In particular cases the reactions of each of the partners were different and far from univocal. It was possible, however, to perceive the general tendency. During spring and the first part of summer the newly settled ants preferred, as their neighbours, Colony K-III to SP-I although they encountered an apparently identical aggressive reception on both sides. However, after a longer or shorter and more or less bitter conflict they usually moved (or were taken) to Colony K-III. (Particular branches managed to exist independently from several days to about a month). Only single individuals moved (or were taken) to Nest SP-I. (It was possible to record this because great numbers of ants were marked with sprayed paint). Only the last two branches, founded on 30 August and 1 September, were absorded by Colony SP-I completely and almost without conflict (within one day). One of these branches had been taken from a polycalic colony J of *F. polyctena*, completely foreign to the former slaves. The adapted ants (marked individuals) were seen on the nest of SP-I even in the spring of the following year.

DISCUSSION

It is a fact that swarms of *F. sanguinea*, a social parasite, are eliminated by slave workers of *F. polyctena* when the abundance of the latter greatly exceeds that of the former. However, the mechanism of this phenomenon remains to be determined. Out of the question is the process reported by MARIKOVSKY (1963) from Eastern

Siberia, namely a division of swarm and formation of something like bispecific oligocalic colonies of *F. sanguinea* and *F. rufa* L. During the experiments in the Gorce Mts. there were absolutely no doubt that the swarms of the social parasite had been dying out. (Incidentally, it is interesting to note how differently the ants reacted to a seemingly identical situation: an excess of slave individuals of red wood ants in *F. sanguinea* colonies). There were no indications that adult workers of *F. sanguinea* had been killed. And they could not have perished due to adverse wintering conditions (a type of nest unsuitable for the species) because in both cases described the mixed swarms overwintered in winter nests of *F. sanguinea*, either exclusively (SP-I) or partly (SP-II).

There remain two probable mechanisms by which *F. polyctena* gets rid of *F. sanguinea* and it seems very likely that both occur together. Elimination of the queen (queens) is one of them, elimination of the offspring is the other.

Elimination (killing) of queens may take place immediately after a mass emergence of slaves (and, in any case, already during the first season when the species live together) or during the next season when ex-slaves adopt conspecific queens. But even if the earliest of the likely periods when *F. sanguinea* queens are killed (and this would mean the latter part of July) were taken into consideration it would not explain the fact why the species begins to die out in the spring of the following year. July is the very time when *F. sanguinea* reproduce. In such a situation at least a small new generation of *F. sanguinea* workers would survive untill late summer. The sexual generation is produced even earlier than that. The nuptial flight of *F. sanguinea* takes place in July on August, yet no flight of alates from the mixed colonies was recorded in spite of observations carried out almost every day.

Therefore, the elimination of *F. sanguinea* queens must have been accompanied (or preceded) by elimination of their offspring. Using a part of offspring as food is common among social insects, including ants (WILSON 1971). It happens in *F. polyctena*, among others when there occurs an overproduction of the new generation in a colony or when there is overpopulation (BUGROVA, pers. comm.). Eggs, larvae, pupae, and even newly emerged imagines may be subject to cannibalism. [Instances of killing young colourless workers by their nestmates within colonies of *F. polyctena* were recorded in the Gorce Mts. (Colony W on the Wyłupki hill) in 1988].

When a quarter million individuals are added to a colony of several thousand or even several dozen thousand ants, the food situation of this colony becomes critical. Therefore it would not be surprising if adult ants began to devour the younger stages. It may be assumed that the alien, and not the conspecific, offspring would be the first to fall victim to the coexisting ants. In this "race" *F. sanguinea*, being far less abundant, stands no chances. So much for hypotheses. This question may be solved satisfactorily only in the course of laboratory experiments.

The next problem is the change, taking place with the passage of time, in the mutual attitude of the swarm of former slaves to their conspecific partners. It seems to be connected with a change in the generation of workers in the "liberated" colony. As long as it is dominated by individuals that had emerged in the nest of *F. sanguinea* and in its presence, the course of their relations with other ants (colonies) of *F. polyctena* is not normal. A colony becomes a typical representatives

of its own species (both in the taxonomic and ethological respects) only when ex-slaves have been replaced by a new generation of workers.

However, it must be pointed out here that even the relations between "normal" *F. polyctena* ants (individuals or artificially founded branches) are very complex. Experiments made in this field provide surprisingly varied results, depending on a great deal of habitat and intracolonial factors (pers. data, not published).

The above-described phenomenon of slave autonomization draws attention to the relativity of the relation: a social parasite–its victim. It is true that the facts presented refer to an artificially created condition and an atypical slave species. However, "atypical" slaves (i.e. species outside the subgenus *Serviformica* FOR.) are said to be recorded in *F. sanguinea* not all that seldom (GALLÉ, pers. comm.). Besides, nothing is really known about the principles on which *F. sanguinea* coexists with its "typical" slaves when the abundance of the latter greatly exceeds that of the former. It does happen that *F. fusca* L. constitutes (in Hungary, locally and periodically; GALLÉ, pers. comm.) up to 70% of mixed colonies. Its chances may be a little better then...

The observations on the functioning of mixed colonies of *F. sanguinea* and *F. polyctena* were made incidentally during the studies on artificial colonization of red wood ants in the Gorce Mts. (PISARSKI, CZECHOWSKI 1990a,b). They have suggested a concept of an entirely new method for colonizing red wood ants – through *F. sanguinea* (of course, only under certain, precisely defined, habitat conditions). This method would be technically simpler than the classical one (!), and from the point of view of ants this would probably be more natural and therefore more successful.

Yet to be explored is the question of the minimum ratio between *F. polyctena* and *F. sanguinea* ants that is indispensable for autonomization of slaves. Appriopriate studies have already been undertaken. However, even obtaining great numbers of pupae of red wood ants does not present a major problem thanks to the PODKÓWKA'S method of wax bee combs (WIŚNIEWSKI 1973, CZECHOWSKI 1989).

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The same phenomenon regarding *Formica pratensis* RETZ. as slaves of *F. sanguinea* was noted by FOREL (1874, 1928).

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STRESZCZENIE

Autonomizacja niewolnic z mieszanych mrowisk *Formica sanguinea* LATR. i *F. polyctena* FOERST. (*Hymenoptera, Formicidae*)

Do dwóch monokalicznych mrowisk *Formica sanguinea* LATR. sztucznie wprowadzono duże liczby poczwarek *F. polyctena*: ok. 230 tys. i 250 tys. Uzyskano mrowiska mieszane, złożone odpowiednio z 96% i 80% (nietypowych) niewolnic. W pierwszym roku istnienia tych mrowisk współbytowanie i współpraca robotnic obu gatunków układały się bezkonfliktowo (CZECHOWSKI 1989). Wiosną następnego sezonu w gniazdach całkowicie zanikała *F. sanguinea*, ex-niewolnice adoptowały młode zapłodnione samice swego gatunku (po locie godowym) i dawniej mieszane mrowiska przekształcały się w normalnie funkcjonujące mrowiska *F. polyctena*. Przypuszczalnie eliminacja pasożyta społecznego następowała w wyniku zabicia samic i zjadania potomstwa *F. sanguinea* przez dysponujące ogromną przewagę liczebną niewolnicze osobniki *F. polyctena*. Eksperymenty i obserwacje przeprowadzono w latach 1987–1989 w Ochotnicy Górnej w Gorcach (Beskidy Zachodnie).