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Mixed polycalic colony of *Formica* (*Serviformica*) *cinerea* MAYR and *Polyergus rufescens* LATR (*Hymenoptera, Formicidae*)

[With 3 Figures]

Introduction

Polyergus rufescens LATR. is very rarely encountered in the territory of Poland. It is possible however, that it is much more common than supposed but its cryptic habits make it difficult to observe. Up to date it has been reported from only few scattered localities in the country. Individual nests of *P. rufescens* in Poland had been found in the following localities: Bielinek in the Chojna district (GRIEP 1940); Białowieża in the Hajnówka district (BISCHOFF 1925); Osiek near Nakło in the Wyrzysk district (TORKA 1914); Puławy (DOBRZAŃSKA and DOBRZAŃSKI 1960); Kazimierz in the Puławy district (MINKIEWICZ 1935, PISARSKI 1953); Kraków (ŁOMNICKI 1923); Ujazd in the Kraków district (KULMATYCKI 1920). There are also known few colonies from the Kampinos Forest near Warsaw (DOBRZAŃSKI in litt.).

P. rufescens is a social parasite practicing "slavery" that is to say carrying away of brood from the nests of certain other species of ants. This type of parasitism in *P. rufescens* is obligatory. Its workers are incapable of feeding themselves alone nor of the rearing of their own progeny and are completely dependent upon the workers of the "slave" species. Most frequently exploited species by this ant is in the first order *Formica* (*Serviformica*) *fusca* L., to lesser extent other species of this subgenus namely: *F. rufibarbis* F. (DOBRZAŃSKA and DOBRZAŃSKI 1960), *F. cinerea* MAYR and *F. cunicularia* LATR. (this last is listed in the literature as *F. rubescens* FOR.), and *F. glebaria* FOR. (WILSON 1971).

How the young queen, after the mating flight, sets up the new nest is a disputed matter (Dobrzański 1965). Regardless of how this is accomplished, whether by killing of the legitimate queen in her "new" nest or its removal by other means from the nest or simply by surreptitious invasion of an "orphaned" colony, the outcome is a mixed society made up of two different species. This condition is further maintained and intensified by occasional plunder by the "master" species of the nearby prospective "slave" colonies.

Observations

A mixed colony of *P. rufescens* and *F. cinerea* was located at Łomna (Nowy Dwór district) on the margins of the Kampinos Forest. It should be mentioned that *F. cinerea* as a polygynic species is most frequently found in the form of extensive polycalic colonies. The above mentioned society occupied typical habitat for *F. cinerea*, a dry, sandy, well sunlit forest meadow about 30 m^2 amidst the forest of young pine trees. The external appearance of this colony was much the same as of the usual polycalic colonies of this species. One of the nests in this colony was occupied by the mixed swarm of *F. cinerea* and *P. rufescens*. The remaining, however, exclusively by its "legitimate" owners (Fig. 1). The behaviour of these ants was investigated in detail on the daily basis.

Typical plunder raids of *P. rufescens* (Dobrzańska, Dobrzański 1960), were carried out during the entire month of August on sunny days between 3 and 5 p. m. The usual time for these raids as a rule is in July but due to the exceptionally rainy summer the ants delayed raiding until the following month. These raids were undertaken by columns of *P. rufescens* exclusively from the nests occupied by their swarms. To their own nest they returned invariably loaded up with booty: pupae and the larvae of the slave species. Frequently these raids followed through the territory of the neighbouring nests of the colony which never became subjected to them (Fig. 1). The raids reached "foreign" nests of *F. cinerea* or *F. fusca* situated 10 to 30 meters away from the attacker's own nest (Fig. 2). Only once a small column of the raiders of *P. rufescens*, about 1000 strong, reached a small nest far out on the margins of the colony and away from the main complex of the nests. The workers of *P. rufescens* surrounded the entrance into the nest. In general confusion, individuals of both species hectically exchanged information through their antennae. There was neither fight nor plunder of the brood and after 15 or so minutes the column of the raiders returned to their own snet and then marched away in another direction.

On the average in these raids took part between 2000 to 3000 individuals in one, less frequently in two columns, in the latter case attacking simultaneously different colonies. Altogether the expeditions went out in five different directions with some routes being rather decisively preferred to others. Most

frequently the columns of these ants moved in the direction of two small colonies of *F. cinerea* where the objects of the simultaneous raiding were several nests located near each other (Fig. 2, A, B). Upon arrival in the vicinity of the colony to be attacked, the columns divided into several clearly defined groups, attacking different nests. Individual ants of *P. rufescens* dispersed more or less evenly over an area of several square meters in order to penetrate many small nests. Expeditions into these colonies were on the whole successful and were

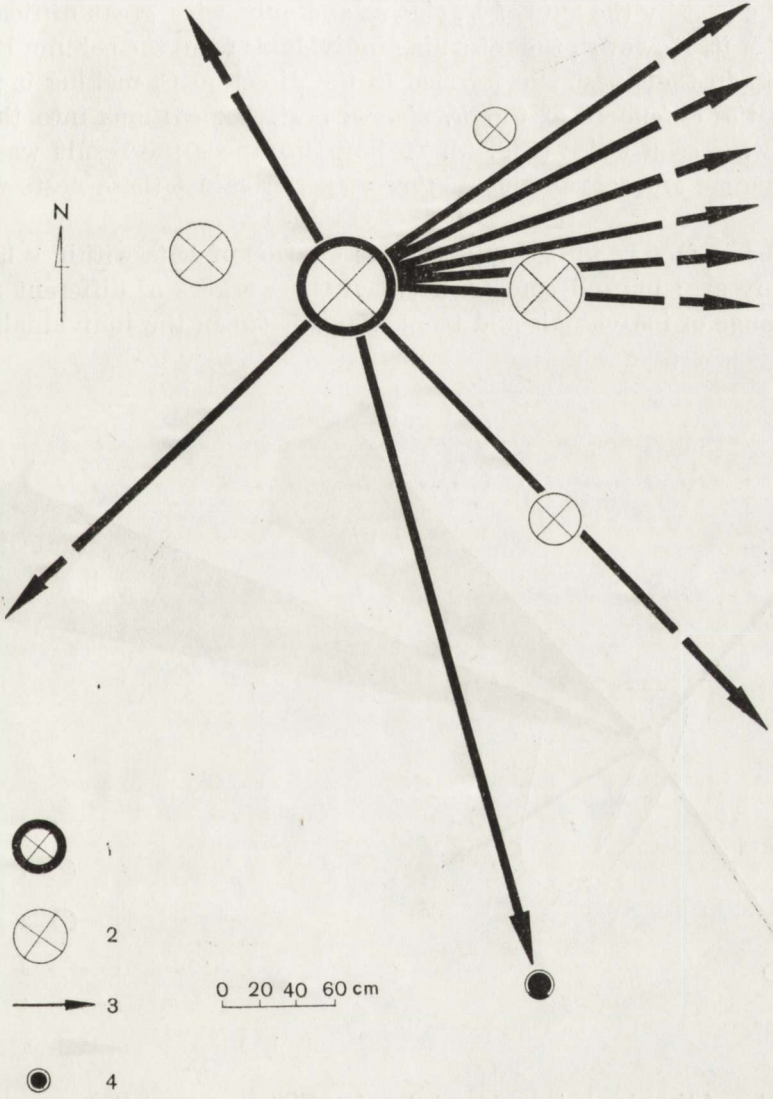

Fig. 1. Fragment of the mixed polycalic colony of *F. cinerea* and *P. rufescens* with the direction of the plundering raids. 1 — mixed nest; 2 — nest of *F. cinerea*; 3 — direction of raids; 4 — marginal nest of the colony.

repeated as much as 3 to 4 times during the day. It was estimated that as many as 10,000 pupae were plundered. The total number of brood (larvae and pupae) carried away from the neighbouring nests during the season should have been between 150,000 to 200,000. Simultaneous plundering expeditions of *P. rufescens* at the same time were despatched in the directions B and C (Fig. 2). While most of the ants from the column attacking in the direction B were returning to their own nest loaded up with booty, only few of those attacking in the direction C got back. This latter column met up with a very strong defense of the nest by the ants of *F. cinerea* and only with great difficulty managed to enter it. However, the returning individuals from the column B deposited their booty in their nest and hurried in the direction C, making it possible to overcome the defenders of the *F. cinerea* nest. Expeditions into the nests of *F. fusca* were seen twice (Fig. 2). In both instances the result was only few hundred pupae and larvae and further attacks against these nests were abandoned.

The basic factors integrating various swarms of ants within a large, polycalic colony are: mutual contact between the workers of different nests, mutual exchange of individuals and trophallaxis between the individuals and bet-

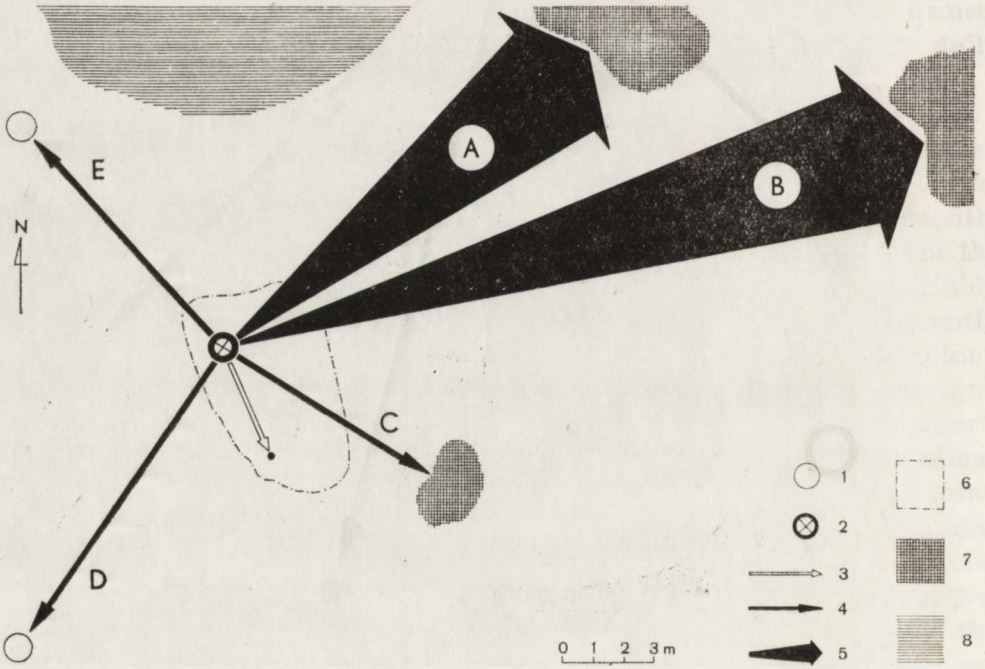

Fig. 2. Routes of the plundering raids of *P. rufescens*. 1 — nest of *F. fusca*; 2 mixed nest of *P. rufescens* and *F. cinerea*; 3 — route of an abortive raid to the marginal nest of the colony; 4 — route of the raid; 5 — main directions of the raids; 6 — territory of the mixed colony of *F. cinerea* and *P. rufescens*; 7 — territory of *F. cinerea*; 8 — territoty of *F. rufa*.

ween different nests. This type of integration got also observed in the above studied, mixed, polycalic society. Different nests communicated with each other throught two very distinct tracks of workers. The individuals of F. cinerea from the mixed nest also had intensive contacts with other nests. The workers of *P. rufescens* were received in a very friendly manner by all inhabitants of the colony. Frequently, single ants of this species lost during the plundering raids or exploring the terrain on their own prior to an expedition either readily entered the nearby nests of the colony or got literally dragged in by the workers of *F. cinerea*. This latter fact was a general rule. Once upon the surface of the nest such ant was dragged out by force by the worker of *F. cinerea* and in the process took up the characteristic position,with curved body and legs. Its transport was similar to the transport of ants among many ant species. The carried ant had its abdomen curved under the body of the "stevedore" who at the some time supported it with its mandibles. Also observed was mass transfer of the brood by the workers of *F. cinerea* delivered by *P. rufescens* from its own nests to the other nests in the colony. Large part of the booty of the slave raiding ants is used by them as food (Dobrzański 1965), therefore this phenomenon should be regarded as a process of the food distribution throughout the entire polygynic society. The individuals emerging from part of the captured pupae were incorporated into the various swarms in the neighbourhood. For example individual ants of *F. fusca* appeared in several nests of the colony, sometime after the plundering expeditions of *P. rufescens* into the nests of this species.

In the polycalic ant colony of *F. cinerea* exists the possibility of more or less even distribution of progeny between different nests, according to their requirements and food supply. This would be particularly important at the time of the intensive fecundity of the queens when feeding of an exceptionally large number of larvae would exceed the capacity of the swarm. In this respect, most difficult is the period of reproduction of the sex forms after their emergence from the pupae when they still remain in great number in the nest.

The mating flight of the sex generation was not observed as it occurs in June or July while studies were carried out in early August. However, mass flight of *P. rufescens* was observed in the middle of August. The dispersal flight occurred at noon when the temperature was about 35°C in the air and nearly 50°C on the surface of the sand. Under the circumstances, the workers of *F. cinerea* normally well adapted to the activity in high temperatures refrained from the exploration of the colony's territory. The emergence of the winged forms of *P. rufescens* took place from all the larger nests of the colony, including those that were occupied exclusively by *F. cinerea*. This shows that the larvae of the sexual forms of *P. rufescens* were distributed between various nests of *F. cinerea*. That way the nest already forced to feed thousands of parasitic individuals got rid of the necessity to maintain an excessive number of social parasites.

It is possible that the breeding of the part of the workers of *P. rufescens* takes place in different nests because on several occasions the juvenile, not completely coloured individuals of this species were seen beeing transferred to their proper nests.

The result of these observations suggests that the above mentioned mixed ant society has special type of social structure. The origin of it probably lies not in the settlement of fecund queen of *P. rufescens* in a single nest of slave species but in the nest of a large polycalic colony. Most frequently exploited ant by *P. rufescens* is *F. fusca* whose societies occur in the monocalic form. However, after the entry into one of the nests of the polycalic colony of the *F. cinerea* the queen of the social parasite had a chance to remove the "legitimate" queen of the host or of several such queens from only this particular nest. The other swarms of *F. cinerea* can retain thus their normal character. Subsequently emerging workers of *P. rufescens* remained in the nest and remained friendly toward the individuals of *F. cinerea* from other nests in the colony because these are permeated by the odour typical of the particular ant society. These in turn did not distinguish the parasitic ants from other inhabitants of the nest. The society of *F. cinerea* probably retained the ability of formation of the filial nests. The nest of this type was probably the one which plundered by an expedition of *P. rufescens* (Fig. 1 and 2). The nest located on margins of the terrain must have lost most of the contact with the remainder of the colony.

The presence of the queens of *F. cinerea* was also indicated by the clear cut differences between the appearance of the workers of such colony and the individuals from other nests which so to speak represented the "reserves" of the slaves. Mixed society had rich supply of carbohydrate food in the numerous concentration of aphids on the nearby pines. Thanks to the plundering raids of *P. rufescens* the entire colony existed in exceptionally good circumstances, having at its disposal huge supply of protein food. The individuals of *F. cinerea* developing in such environment were exceptionally large, much more so than in the other societies in the area, which were systematically plundered and damaged by the raiders. Since the slaves are carried away from their own maternal nests most frequently as pupae or terminal larval stages or occasionally even as young adults, their size is already determined. Thus it was possible to determine the origin of an individual in a colony with considerable degree of probability. This suggests that most of the "foreign" brood in the nests of *F. cinerea* carried therein by *P. rufescens* was simply eaten there and then. On the other hand, there was no sudden increase in the population of the nest after succesful raids. The increasing demand for workers in the nest taken over by the social parasite could partially be supplied by the influx of the workers of *F. cinerea* from other nests in the colony. This was no doubt reflected in the greater than usual consumption of larvae and pupae. For example, two expeditions of *P. rufescens* into the nests of *F. fusca* brought back about 1000 specimens of booty. Following these raids only 2–3 individuals of this spe-

cies could be seen simultaneously in the area. Moreover, the workers of *F. cinerea* regarded such ants of *F. fusca* with suspicion and there was difficulty in the communication between them.

It may be said that the mixed polycalic society was made of the queens of both species (one of *P. rufescens* and several of *F. cinerea*), co-existing in the nest on an equal and independent entity, the progeny of these queens, the slaves of *F. cinerea* and a small number of *F. fusca*. There was a definite possibility of contact between the ants of two groups with the exception of the queens of both species (Fig. 3). The above decribed special case of social parasitism has very special features. Certainly, the slave making proclivity of *P. rufescens* is harmful to *F. cinerea* as well as to the other parasitized species of ants. But the interaction of the two sides in this exceptional situation are pro-

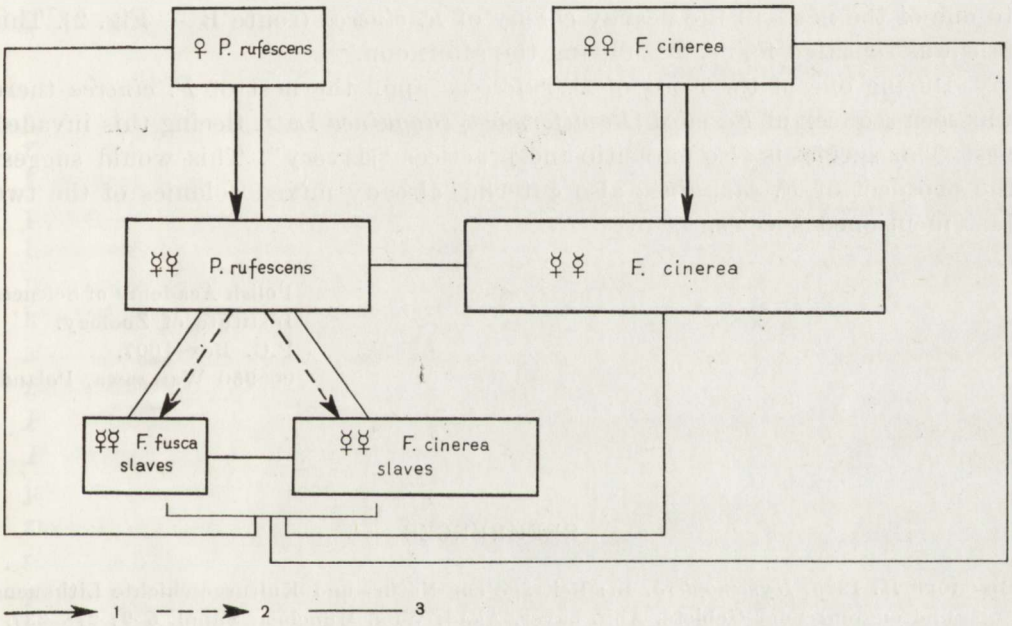

Fig. 3. Outline of the social structure in the mixed colony of *F. cinerea* and *P. rufescens*. 1 and 2 — genetic interconnections (1 — progeny, 2 — slaves); 3 — contacts between individuals of different groups.

bably advantageous. The parasite, *P. rufescens*, initially weakens the ecological potential of its host very little. While it eliminated from the reproductive function one nest in the colony, it influenced its development by the decisive improvement of the existing conditions by magnification of its food supply and its working force.

A swarm of *P. rufescens* has no prospect of overrunning the entire colony of *F. cinerea*. It is monogynic (ZAKHAROV 1972). Therefore, a single queen inhabiting the nest does not threaten other queens of *F. cinerea* living in other nests

of the colony. The structure of such mixed society is stable and remains so until the death of the queen of *P. rufescens*. After the dying out of thus orphaned swarm of the social parasite, the colony of *F. cinerea* recovers its original structure. There is indeed a possibility of adaptation of a young queen of *P. rufescens* in another nest after its mating flight. In this case the situation in the nest would be exceptional. Two monogynic swarms would blend throught the polycalic society of the host species. In such instance it would be impossible to predict their mutual attitudes toward each other because ants from different monogynic societies are hostile toward each other (PISARSKI 1973).

In the following season the appearance of the mixed colony did not change much. The "slaves" of *F. cinerea* were still in the minority among the ants of this species. This fact supports the supposition that queens of *F. cinerea* were present in the mixed society. At the time one plundering raid was observed to one of the nests in the nearby colony of *F. cinerea* (route B — Fig. 2). This raid was repeated four times during the afternoon.

During one of the raids of *P. rufescens* upon the nest of *F. cinerea* there was seen a queen of *Formica* (*Raptiformica*) *sanguinea* Latr. fleeing this invaded nest. This species is also parasitic and practices "slavery". This would suggest the prospect of *F. sanguinea* also entering already mixed colonies of the two just mentioned species.

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STRESZCZENIE

[Tytuł: Mieszana kolonia polikaliczna *Formica* (*Serviformica*) *cinerea* Mayr i *Polyergus rufescens* Latr. (*Hymenoptera*, *Formicidae*)]

W roku 1973 znaleziono w Puszczy Kampinoskiej w pobliżu miejscowości Łomna (pow. Nowy Dwór) szczególne mieszane społeczeństwo *Polyergus rufescens* Latr. i *Formica* (*Serviformica*) *cinerea* Mayr. W skład typowej polikalicznej kolonii *F. cinerea* Mayr wchodziło jedno mrowisko opanowane przez pasożyta społecznego. Osobniki *P. rufescens* Latr. organizowały wyprawy rabunkowe do okolicznych, obcych mrowisk *F. cinerea* Mayr i *F. fusca* L., nigdy nie napadając na sąsiednie gniazda kolonii. Stwierdzono, że w mrowiskach kolonii zajmowanych wyłącznie przez *F. cinerea* Mayr były obecne również samice tego gatunku, do których nie miała dostępu samica *P. rufescens* Latr., zamieszkująca tylko w jednym z gniazd mieszanego społeczeństwa. Osobniki *P. rufescens* Latr. były traktowane jednakowo przyjaźnie przez robotnice *F. cinerea* Mayr, zarówno z opanowanego przez pasożyta społecznego gniazda, jak i z pozostałych mrowisk kolonii. Znoszone do gniazda *P. rufescens* Latr. zrabowane potomstwo było w większości zużywane jako pokarm i równomiernie rozprowadzane po wszystkich mrowiskach kolonii. Wychów młodego pokolenia płciowego *P. rufescens* Latr. odbywał się również w wielu mrowiskach, co stwierdzono podczas obserwacji lotu godowego.

Резюме

[Заглавие: Смешанная поликалическая колония *Formica* (*Serviformica*) *cinerea* Mayr и *Polyergus rufescens* Latr. (*Hymenoptera*, *Formicidae*)]

В 1973 году на территории Кампиносской пущи около местности Ломна (повят Новый Двур) обнаружено особое смешанное сообщество *Polyergus rufescens* Latr. и *Formica* (*Serviformica*) *cinerea* Mayr. В состав типичной поликалической колонии *F. cinerea* Mayr. входил один муравейник, занятый общественным паразитом. Особи *P. rufescens* Latr. устраивали набеги на соседние чужие муравейники *F. cinerea* Mayr

и *F. fusca* L., но никогда не нападали на соседние гнезда колонии. Констатировано, что в муравейниках колонии занятых исключительно *F. cinerea* MAYR присутствовали также самки этого вида, к которым не имела доступа самка *P. rufescens* LATR., живущая только в одном из гнезд смешанного сообщества. Рабочие муравьи *F. cinerea* MAYR одинаково дружелюбно относились так к особям *P. rufescens* LATR. из занятого общественным паразитом гнезда, как и к особям из других муравейников колонии. Захваченное и приносимое к гнезду *P. rufescens* LATR. потомство употреблялось в большинстве случаев как корм и равномерно распределялось по всем муравейникам колонии. Воспитание половых особей *P. rufescens* LATR. отмечено также во многих других муравейниках, что было констатировано во время брачных полетов.

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