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PROBLEM OF BEHAVIORAL PLASTICITY IN SLAVE-MAKING AMAZON-ANT *POLYERGUS RUFESÇENS* LATR. AND IN ITS SLAVE-ANTS *FORMICA FUSCA* L. AND *FORMICA CINEREA* MAYR

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Abstract. Changes in the natural behavior, expressing adaptation to cohabitation in a community, were observed in the slave-making ants *P. rufescens* and the slave-species *F. fusca* and *F. cinerea.* After a few raids, the initially undirected arousal evoked in the slaves by the amazons' raids, begins to acquire attributes appropriate to the situation, but completely different in both studied slave-species. *F. cinerea* picks up the pupae abandoned on the nest by the slave-making ants and eventually begins to wrench them away from the amazons arriving with prey. *F. fusca,* whose nests have openings so narrow that it prevents the mass entry of amazons with prey, begin to enlarge those openings shortly after the amazons return. After a certain number of raids, *F. fusca* begin to enlarge the openings immediately after the departure of the amazons for the slave-raid. The amazons, on their side, adjust soon to the specific behavior of the given slave-species; in nests with *F. fusca,* they make use of enlarged openings, carrying their prey through them into the nest; when *F. cinerea* are the slaves, most of the amazons begin to drop the pupae on the nest, and later even surrender the prey to the slaves who meet them. It is supposed that in all three species, under the influence of specific conditions there occurs the process of learning of new forms of behavior.

INTRODUCTION

Social parasitism in ants is the only biological phenomenon of its kind and as such it can and should be a source of scientific inspiration

not only for ethologists and evolutionists, but also for theorists of general biology. The importance of social parasitism to the process of theory building was already appreciated by Darwin. Unfortunately, this phenomenon has not been yet thoroughly investigated and almost every attempt to describe it scientifically produces different and frequently controversial opinions. What is more, the opinions on some aspects of *P. rufescens'* behavior are contradictory (e.g., the issue of raid-making mechanisms), and after many years of studies we have even begun having serious doubts about some opinions hitherto regarded as indisputable. It concerns, among others, the widely held opinion about the lack of behavioral plasticity in the amazon-ants.

The only social function performed by *P. rufescens* ants is raiding the nests of the *Serviformica* species with the aim of abducting and bringing back new slaves in the form of pupae. The whole behavior of those ants is subordinated to this one goal. It is therefore understandable that the studies on *P. rufescens* have been primarily or exclusively concerned with the elements of behavior connected with the raids. They are characterized by an established, stereotyped manner of operations with hundreds of soldiers which enables the column to move at an extremely fast pace and which gives the invaders a great advantage over the enemy (5, 8). The stereotyped manner in which those raids are carried out has been influential in the shaping of the opinion that the amazons have little behavioral plasticity and operate on the basis of a rigid chain of reactions. Thus Forel wrote about "blind instict of *Polyergus*" (8, p. 189); also in one of our works (5) we spoke of the "rigity of behavior and lack of plasticity" in *P. rufescens*. But with more research being done on this species serious doubts arise about the correctness of such an one-sided view.

In search of manifestations of plasticity in the slave-making ants we have analyzed those aspects of their life which can be regarded as demanding most plasticity — i.e., the aspects of their social coexistence, or specifically in our case, the cooperation with slaves during the raids. In order to distinguish the aquired adjustments from the inborn ones, we have searched for possible differentiation in the slave-making ants' behavior contingent upon the possession of a given species of slaves, i.e., for differences dependent on the reactions of nestmates with whom the amazons come into contact in various situations of social coexistence and cooperation. We have studied comparatively the behavior of *P. rufescens* living in colonies with one of two frequently occurring slave-species which differ sharply in their behavior: *F. fusca* L. and *F. cinerea* Mayr. Changes in slave-ants behavior were also simultaneously observed.

The basic biological facts about the studied slave-species

Formica fusca L. It is a timid ant who seldom fights, usually reacts to danger by flight, and when raided in its own nest it carries its offspring away. A proportion of the fleeing workers and nurses with the offspring escape in the upward direction, taking refuge on any protruding objects, mostly on grass blades. In the case of attack by the ants *P. rufescens* it is a very effective form of defence because the amazons never pursue the escaping ants.

Those attributes of *F. fusca* are also reflected in the structure of their nests. The nests are carefully concealed and have one or, at the most, two to three exit holes placed close to each other, hidden in the grass and scrupulously covered with grass blades and twigs. In this way there are only narrow slits left on the outside through which only a single ant can pass. This species is not very predacious, the ants do not help each other in transporting the prey and the foragers usually being in only a small prey, which does not interfere with squeezing through the narrow entry hole. There is only a sporadic movement of workers around the nest; for most of the time all is quiet. Under the circumstances, the nest of *F. fusca* is virtually indetectable by sight. The entrance holes are full open only once in the year: during swarming, when the workers uncover and extend them.

Formica cinerea Mayr. Both the biological characteristics and the behavioral attributes of this species add up to a completely different picture. It is a polycalic ant, which means that it builds multi-nest complexes. Numerous daughter-nests are built around the original mother-nest linked with it and among themselves by strong community ties. The inter-nest relationships have not been thoroughly studied in *F. cinerea,* but only in other polycalic species of the same genus: *F. rufa* group (14), and *F. exsecta* (4, 10). On the basis of numerous observations we have reasons to believe that in principle they resemble those found in *F. cinerea.* It means, simplifying slightly, that all nests of the colony have a common, interchangeable working caste. The nests are not made up of permament set of individuals; the worker can work in any nest and is treated everywhere in the colony as an equal nestmate.

Probably the polycalic way of life is responsible for the sense of security in those ants. Their colonies occupy sometimes very large areas, completely controlled by their inhabitants. There is a continuous movement throughout the entire area of the colony. *F. cinerea* know how to fight when raided in their own nests and being excellent building workers, they frequently employ a defensive tactics of barricading themselves inside their nests. Of course, with barricading tactics it is possible

to achieve certain results in the form of saving a part of the nest only when raided by *F. sanguinea*. This form of defense cannot be employed against the raid by *P. rufescens* because they seize a nest in a few seconds, which does not allow the raided ants enough time to dig themselves in.

METHODS

Marking. The most active ants in a given nest were initially marked with dye. It was impossible to mark the ants with wire rings during the observation because with this method it is necessary to catch the ants which in the circumstances inevitably raises alarm in the nest and upsets the whole situation. Marking with dye, on the other hand, has the advantage that it can be done while the ant is running; but in our case it proved particularly difficult, so, as a result, only a limited number of individuals were marked in every nest. The difficulty was mainly due to the fact that the individuals to be marked were highly aroused and that all three studied species move very fast, particularly *F. cinerea,* which belongs to the fastest Polish ants. When there are a great many ants moving around at a fast pace, the marking is further limited by the fact that it is possible to touch a given ant with a grass blade (used as a paint-brush) only once; if the ant is not painted at the first try, the attempts to mark it should be abandoned because of the possibility of making a mistake in a dense crowd and also because chasing after the ant always causes alarm, and aggression and upsets the situation. Whereas a quick, single touch, is not noticed by an aroused ant.

As far as the circumstance permited (i.e., in cases when the same ant was found in another situation before the dye had come off) the marking was suplemented by a wire ring. The marking of the slave-making ants with rings is more difficult and time-consuming than the marking of other species. The trouble and the loss of time is caused by the fact that the captured amazon-ant drives its thin mandibles into the experimenter's finger and it is impossible to pull it off without damaging it. Practically speaking, one ought to wait till the ant loosens its grip and see that it does not cling to the finger in another spot before being shaken off. So the number of amazons to be marked with rings should be kept to a necessary minimum. With short-term observations (i.e., lasting several days) the marking should be confined to the dye method only.

Lately, besides using the old method of attaching the wire rings (7) we also introduced a new method by which the rings are fixed to the legs; this creates great possibilities for distinguishing individual ants. It

is a more difficult method than putting the rings on the petiolus and yet it is still feasible when the following rules are adhered to: the ring should not be put over the tarsus, as it is practically impossible to make several turns with the elastic noose around the joints of a very restless ant; a large noose should be put over the knee onto a bent leg, and then the flexible tarsus can be pulled out from the noose with a thin needle (Fig. 1). In this way only the tibia is left inside the noose. The noose

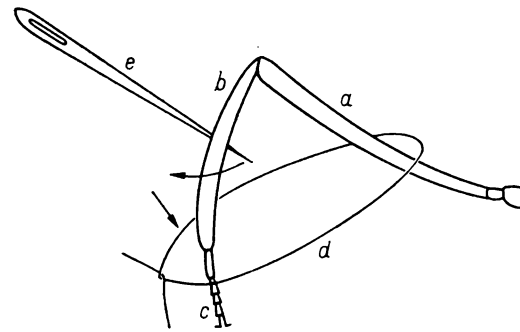

Fig. 1. A method of putting on a ring and pulling the tarsus out of a noose. *a*, femur; *b*, tibia; *c*. tarsus; *d*, wire ring; *e*, a needle.

can be either left on the tibia or moved onto the femur and lightly tightened, as it is done on the petiolus. The noose, of course, can be put on different legs and also on several legs at a time. If only wires of no more than 0.1 mm in diameter are used, they do not interfere with the ants' agility.

Materials. Direct observation of the studied ants' behavior during the whole season of the amazons' raid-making activity were repeated several times an the nests shared by the amazons with each slave species. The observations of the *P. rufescens*' nests with *F. cinerea*-slaves were carried out over the period of 2 years, on two nests each year, and two nests with *F. fusca*-slaves were under observations over 3 years. In all, the observation and research records are made up of recordings obtained during 10 seasonal studies. During each season about 70–80 raids have taken place. Since publishing the full text of all the records is impossible and would not serve the purpose, we shall exemplify them only in the form of a diagram which presents one season for each species. All collected recordings enabled us to reconstruct a typical cycle of changes occurring in the course of one season in the behavior of the slave-making ants and their two slave-species. This typical, average cycle is presented in a descriptive form and also in the form of a diagram.

RESULTS

Already the initial observations of the *P. rufescens* ethological adjustment to social coexistence with two very different slave-species have revealed a certain regularity. The slave-making ants do not always bring the carried prey inside their nests, but some times abandon the captured pupae on the nests' surface leaving it to the slaves to take further care of them. A similar phenomenon was also observed by Beck (1). At first sight it seemed that such a behavior was caused by the abundance of the prey, but further analysis of the phenomenon has not confirmed it. It turned out that large-scale abandonment of the pupae outside the nest occurs regularly in those amazons' nests which have *F. cinerea* as slaves. In nests shared with *F. fusca,* even when the prey is plentiful it seldom happens that the amazons abandon the pupae when hurriedly returning to a raided nest for more prey. Upon closer observation we are inclined to consider the abandoned pupae as dropped accidentally in a hurrying dense crowd, which always happens when the prey is plentiful.

It was necessary to find the reason of the differences in the behavior of soldiers belonging to the same species. To this end, close observations and studies begun on the mutual relationships between the slave-making ants and their slaves during the raids and on possible differences in the reaction of both the studied slave-species.

Mutual relations in the behavior of the amazon-ants and their slaves Formica cinerea Mayr during successive raids

The following is an account of typical, cyclic changes in the behavior of the slave-making ants and their slaves in the course of one raid-making season.

At the end of June or at the beginning of July the first amazons appeared on the surface of the nest and after 3 to 4 days the first raid took place. The first marching of the amazons' army out of the nest always brings about the state of high arousal in the slaves which manifests itself in a hurried running about the surface of the nest and in increased aggression. Some manifestations of aggression are described below. Ten to fifteen minutes after the army had marched off the excitement died out, things quieted down and the redundant workers went back to the nest. By the time the army came back with the prey (normally some 25 to 40 min later) the nest had already regained its normal appearance: the worker moved calmly around its surface or dug in the numerous holes and tunnels, which is the usual occupation of *F. cinerea.* Most of the

returning amazons tried to get inside the nest which resulted in a concentration of pupae-carrying ants around the hole through which the army had previously marched out. However, some of the slave-making ants (between 15 and 20) immediately on returning to the nest droppe their prey on its surface. Yet the relatively few workers present at the time on the surface of the nest became once again the state of excitenent when the amazons returned in great numbers, carrying prey. Running around the surface of the nest they would come across the abandoned pupae, get hold of them and take them inside the nest, from the depths of which other aroused workers ran out, increasing the commotion and confusion. It is characteristic of *F. cinerea* that in contrast to the amazons they take the prey to different entrance holes and even to different nests — when the prey is particularly plentiful. But the majority of the aroused slaves, would seize and drag into the nest not the pupaes but the amazons crowding on the nest's surface. Such behavior could be observed in slaves at an earlier time, when the amazons were leaving the nest before going on a raid (13). The slave-making ants react to it in different ways. Although the majority submit to such treatment by the slaves, the reactions of individual amazons can be very different. One ant, for example, was so docile that when a slave pulled it by the leg, the ant entered the nest first, overtaking the guide who still held to its leg. A resistant ant, to give another example, struggling with a slave caught it by the jaws; in obedience to that specific signal, the slave curled up in a suitable posture (5) and allowed the amazon to carry it into the nest.

When pulled by the slaves, the amazons returning with prey frequently dropped the carried pupae, which lay on the ground to be picked up by other workers who happened to run across them. Things were similar during the subsequent raids, but every day the slaves got into the state of arousal faster and in greater numbers. Soon the excitement became visible already on the arrival of the first few slave-making ants with prey although they did not make a crowd or cause a commotion. Also, more and more workers would start picking-up the abandoned pupae. On the raids 3 and 4, the number of *F. cinerea* picking-up the pupae reached several dozens, and while they were engaged in that activity it was possible to mark 15 to 20 of them. Marking a number of *F. cinerea* allowed to keep under systematic observation the same individuals among the slaves aroused by the marching out of the army and by its return. During the subsequent raids, there occurred continuous quantitative changes in the ants' behavior: with every raid there was an increase in the number of pupae-picking slaves in the ranks of the slaves who went out to meet the army, but simultaneously more and more

amazons dropped their prey on the nest's surface. As a result, the slaves were unable to cope with collecting all the dropped pupae which would be seen lying on the ground as late as by the raid 7 or 8. Although sporadically, it still occurred that the amazons itself were dragged into the nest by the aroused slaves, which paid no attention to the pupae dropped on the occasion. During that period, up to about the raid 10, there occurred more and more obvious qualitative changes in the behavior of both the slaves and the slaves-making ants. *F. cinerea* were beginning to show increasingly the signs of excitement even before the return of the army, moving around the nest in large numbers, aggressively disposed. With the arrival of the first returning amazons they rushed towards them and snatched from them the prey — which the slave-making ants were quite willing to give up anyway; that was the reason why no more abandoned pupae could be seen around. Only a few individual soldiers carried the prey themselves into the nest. The arousal of *F. cinerea* was by now quite clearly directed exclusively onto the pupae. It happened occasionally that a slave dragged to the hole an amazon carrying a pupa but as soon as the amazon dropped the prey in the commotion, the slave would immediately release the dragged ant, and instead get hold of the pupa and take it to the nest.

Changes in the *F. cinerea*-slaves reactions in an exemplary nest are shown in Fig. 2. The average changes estimated on the grounds of all observations are presented in Fig. 3. Figure 4 presents the simultaneously occurring changes in the behavior of the slave-making ants *P. rufescens*.

Mutual relations in the behavior of the amazon-ants and their slaves Formica fusca L. during successive raids

The first marching out of the slave-making ants' army gives raise to phenomena similar to those occurring in a nest with *F. cinerea*-slaves, the only difference being that a greater number of slaves emerge from the depths of the nest (normally there are only very few of them on its surface). Such numbers of the *F. fusca* workers at a time can be seen only during the nuptial-flight.

As in *F. cinerea,* the excitement would die out after the columns of amazons had marched off, and the nest would regain its normal appearance until the army came back with the prey, which would again provoke a state of indirected arousal in the slaves. The slave-making ants carrying the captured pupae headed straight for the hole through which the army had left, so that around it collected a dense crowd of ants which pushed ahead holding the pupae in their mandibles. It happened some times that, due to a particularly small entry hole to a *F. fusca* nest, some pupae were dropped. They usually remained on the ground quite

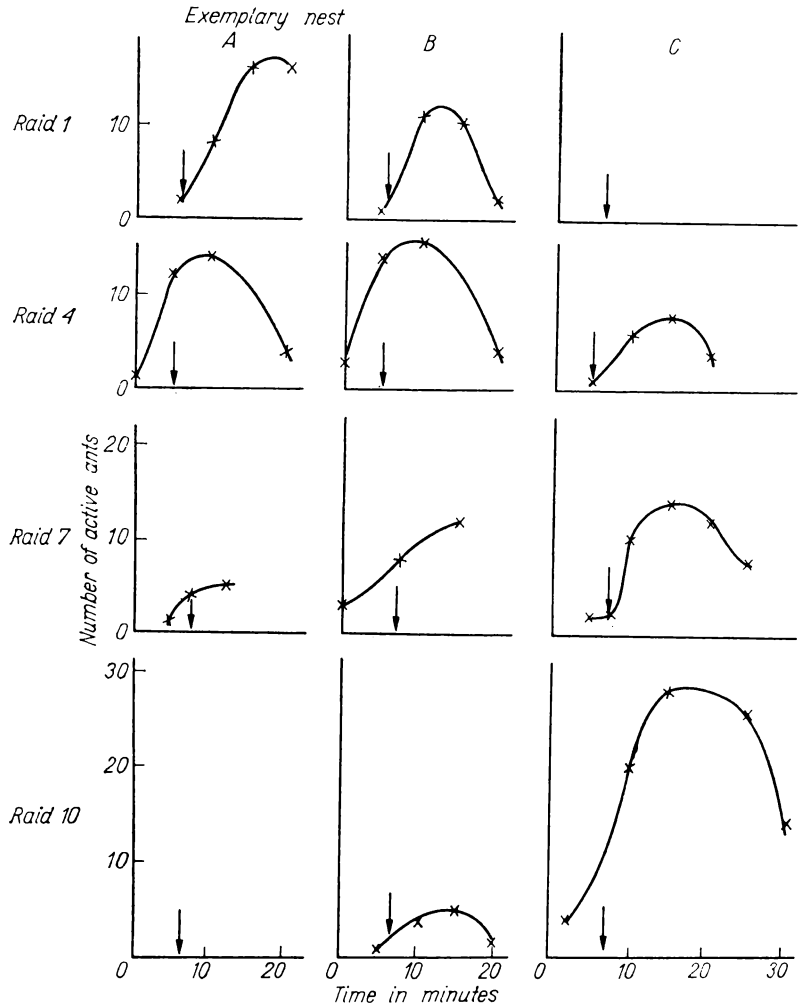

Fig. 2. Changes in the reactions of *F. cinerea*-slaves from the nest 1 to the successive *P. rufescens'* slave-raids. *A*, number of slaves dragging pupae-holding amazons to the nest; *B*, number of slaves picking up pupae abandoned by the amazons; *C*, number of slaves wrenching pupae away from the amazons. Time is measured from the return of the first pupae-carrying amazons. The arrow, the mass arrival of amazons with pupae.

a long time before being collected by some of the slaves running around and over them, which differenciated the behavior of *F. fusca* from that of *F. cinerea*, as not each of the *F. fusca* workers would pick up the dropped pupae. It happened that several or more slaves run over a pupa before one of them took it along. Infrequent instances of a slave trying to wrench the prey away from an amazon occurred only during the

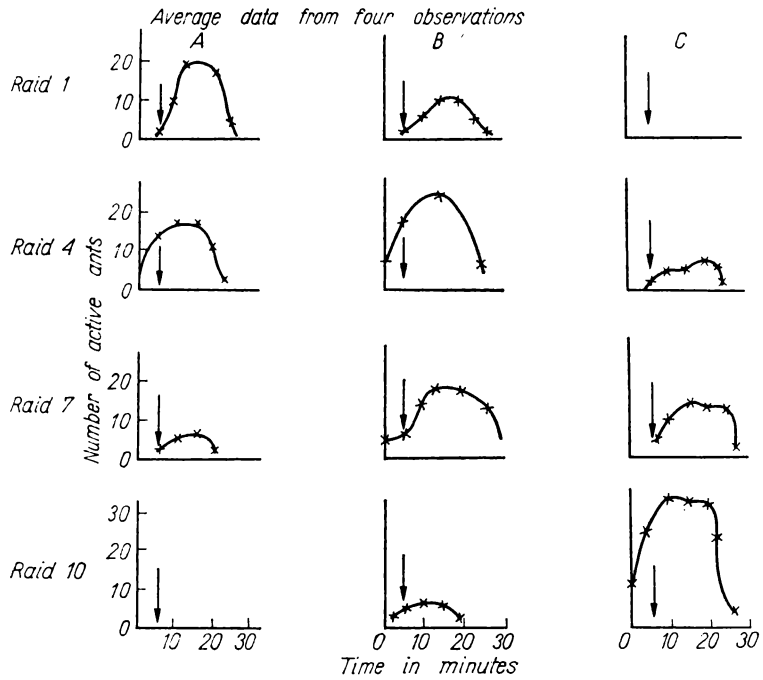

Fig. 3. The average changes in the reactions of *F. cinerea*-slaves to the successive *P. rufescens*' slave-raids. *A*, slaves dragging pupae-holding amazons to the nest; *B*, slaves picking up pupae abandoned by the amazons; *C*, slaves wrenching pupae away from the amazons. Time is measured from the return of the first pupae-carrying amazons. The arrow, the mass arrival of the amazons with pupae.

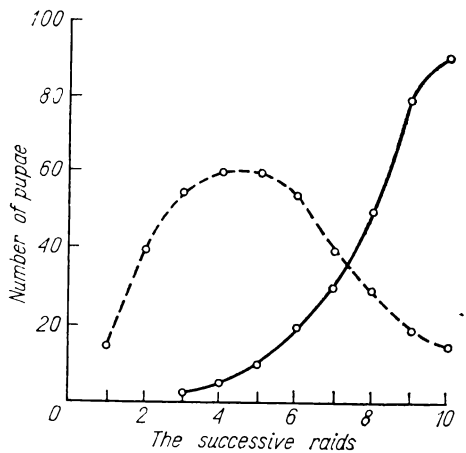

Fig. 4. Changes during the successive slave-raids in the behavior of *P. rufescens* with *F. cinerea-slaves* (the data is approximate for methodological reason). Dashed line, the pupae abandoned by the amazons; continuous line, pupae given up to slaves trying to wrench them away.

first few raids not to reappear later. It is hardly ever seen that an amazon should surrender its prey voluntarily and without a struggle which is a very common occurrence in the nests with *F. cinerea*-slaves. Most often *F. fusca* relinquished the pupa strongly held by the slave-making ant, after trying to pull it away once or twice.

With every attack there was an increase in the number of slaves aroused by the attack, and the indirected character of that arousal manifested itself in the fact the *F. fusca* known for their mild disposition, were vigorously attacking and painfully biting the observer. Naturally the observer tried to keep away from the road along which departs an amazons' army, but, in spite of that, the *F. fusca* went for him and turned their aggression against him. During the research on independent nests belonging to this species those ants seemed incapable of such violent and active aggression and even physically incapable of piercing the human skin with their mandibles. Besides, all formerly studied *Formica* species, including also the *F. fusca* from the studied nest, got used in a few days to the observer's presence and crawled onto his hand — except the above-described situation — without any signs of aggression or fear.

During the first few amazon raids the excitement of *F. fusca* similarly to *F. cinerea,* decreased in the period between the army's departure and its return. While the amazons were pushing their way towards the only entrance holes to the nest after the return from the raid 1 or 2, it could be observed that one or two workers tried to pull away the building material covering the hole. During the raid 3 or 4 the aggressiveness of *F. fusca* which decreased after the army's departure, started to grow again before the army was actually back. By the raids 4 and 5 it is evident that the slaves are uncovering cleaning the entry hole immediately after the return of the amazons with prey. Later, the arrival of the first few amazons was enaugh to induce a similar building activity on the part of one or two slaves. Eventually, during the subsequent raids the slaves started to pull away the building material covering the hole even before the return of the first prey-carrying amazons. Beginning with the raid 10 or 11, the slaves' arousal induced by the army's *exit* from the nest, was directed from the start towards uncovering of that very hole through which the army left. It is especially remarkable that the increase of this activity is accompanied by the disappearance of *F. fusca'* aggressiveness, previously noted in that situation. Even the seizure of workers unblocking the hole does not now arouse the ants — the remaining ants calmly keep on working.

After the raid 10, the following experiment was repeated several times in order to check whether the necessity to let in quickly the

crowding amazons with prey was a direct stimulus for the slaves to uncover the hole. The moment the army returned and the amazons started to enter the nest through the hole enlarged for this occassion, it was covered by the observer. This forced the rest of the army to move around the nest in search of another entry. When after a moment of confusion the slave-making ants began to crowd in large numbers around another nearly hole (covered, of course, with building material) — the slaves immediately gathered at the same hole. After half a minute first one worker, and soon afterwards the others set about uncovering the hole, removing the blocking material.

A similar event, but one that occurred naturally, was also observed. The road along which the amazons returned with the prey led to a completely closed nest-hole, through which they used to leave on raids some weeks before. Te amazons converged on the closed hole, trying to get inside, which shows that they have a memory for places. The aroused slaves came to the place immediately. Two of them (one of the ants has been earlier marked as a forager) took the pupae away from the amazons (or picked them up from the ground — it has not been noticed by the observer) and carried them to a hole already uncovered, at a distance of 8 cm, through which the army was set off on the raid. The crowd of the slave-making ants remained, however, by the closed hole — and after a while one, and then another *F. fusca* began pulling twigs out of it. Most amazons took the prey inside through that hole, which was being actually widened by the slaves and went off for more prey to the raided nest. When the ants returned, the new hole had already been fully opened and the army carried the prey inside through both the newly opened and the old hole.

Sometimes, when the prey was particularly plentiful, the strongly aroused *F. fusca* started spontaneously to clean a second and even a third hole nearby. If the distance between them did not exceed several centimeters — the amazons, crowding around the main hole were likely to come across the neighboring holes and make use of them. When that did not happen, other workers would cover back the unused open hole. It might happen that such a hole was both uncovered and covered at the same time. In the end, however, the influence of currently operating stimuli prevailed and the workers who were removing the building material from the unused hole gave up their work. Very quickly and without a conflict, on the other hand, commenced the barring of the hole in the evening, right after the last prey had been brought inside the nest. Individual slave-making ants, returning late, with or without prey, had to squeeze through the narrow passages, without evoking any reaction on the part of slaves who were closing the holes. In one case, the process

of closing the hole after the raid 17 has been interrupted in a curious way. The opening was nearly closed, when a *F. fusca* worker emerged from the nest and removed a twig recently placed over the hole by its nestmate. A single aroused amazon ran out of the nest and after running on the surface for 8 min, returned to the nest, upon which the hole was closed. Evidently its arousal inside the nest must have caused the hole — uncovering activity in the slave.

Figure 5 shows changes in the building behavior (uncovering of holes)

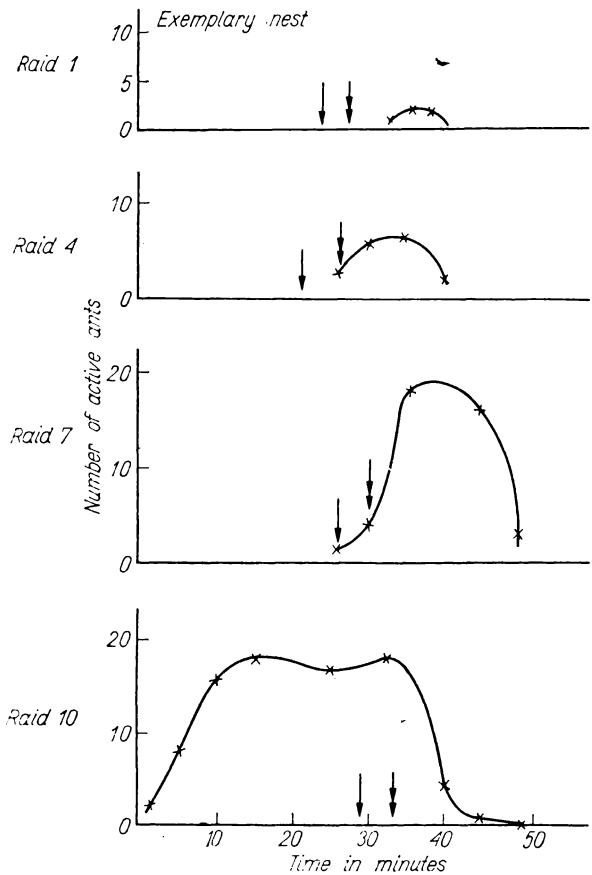

Fig. 5. Changes in the building activity of *F. fusca*-slaves from nest 2 during the successive *P. rufescens'* slave raids. Time is measured from the marching-out of the amazons' army from the nest. The arrow, the return of the first amazons with pupae; double arrow, the mass arrival of the amazons with pupae.

of *F. fusca*-slaves, in an exemplary nest, and Fig. 6 — the average changes estimated on the grounds of all observations.

Two very clear examples of displacement activity were observed.

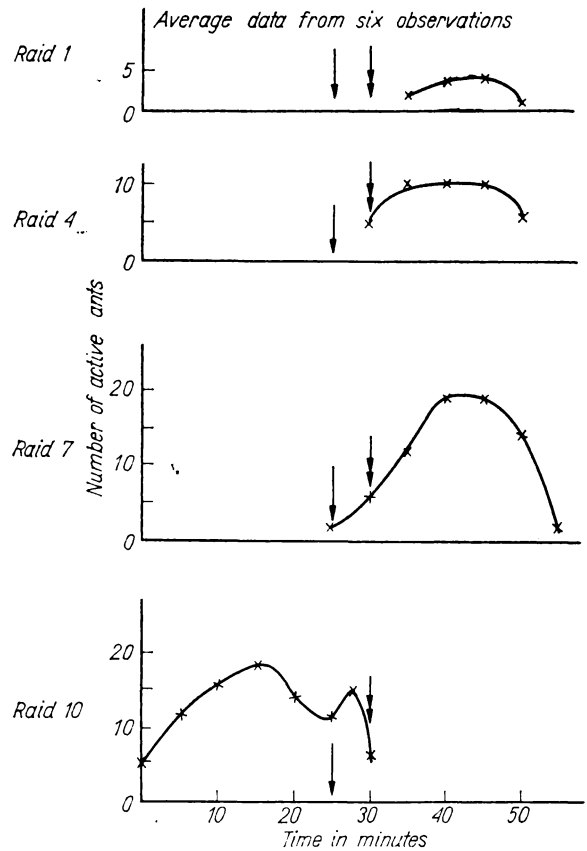

Fig. 6. The average changes in the building activity of *F. fusca*-slaves during the successive *P. rufescens'* slave-raids. Time is measured from the marching out of the amazons' army from the nest. The arrow, the return of the first amazons with pupae; double arrow, the mass return of the amazons with pupae. For the sake of clarity the time of amazon's return in raids 1, 4 and 7 is arbitrarily determined as in raid 10.

During the season there are days when the slave-making ants do not make raids. Later in the season, on such days some *F. fusca*-slaves undertook additional barring of the otherwise closed exit holes, which activity occurred around the marching time of the army, i.e., at the most active time of day. Obviously, there must have been then sharply conflicting tendencies in the behavior of individual ants.

The second example relates to the partial removals in the examined nests which occurred twice during the above-mentioned studies. They took place once in the nest with *F. fusca*-slaves and once in the nest with *F. cinerea*. In both these cases there was a clearly observable increase in the removal-related slaves' activity during the period of arousal between the army's departure and its return.

DISCUSSION AND CONCLUSIONS

There is little mention in the literature on the subject of mutual relationships between the amazons and their slaves. We have found only one experimental study — by Sakagami and Hayashida (12), who studied the influence of the amazons' presence on the building activity of *F. fusca*-slaves. The authors supposed that the mere presence of a single slave-making ant of a *F. fusca* worker should influence the speed of sand-digging by building individuals, but the results did not confirm their hypothesis.

The existence of marked behavioral influences which social parasites have on their slaves must have been noticed by Forel (8) because he mentioned that "slaves *retain certain specific attributes* of behavior characteristic of their species". Unfortunately, he does not give more detailed information. The present studies have revealed that social parasites affect the behavior of slaves. Initially, the amazons' raids induce in the slaves only a state of high, undirected arousal evidenced by increased bustle and aggressiveness. It is the only situation — as confirmed by dozens of years of observations — when *F. fusca* attack human beings. The displacement activity is manifested also in the increase of removal during such a period of arousal, which phenomenon was also observed by Czechowski (3).

At the beginning of the raid-making season there exist two separate peaks in the general arousal of slaves, induced by the amazons' raids: during the army's departure from the nest and during its *return* with the prey — with a clear break during the army's absence from the nest. After several raids, the duration of arousal extends beyond the periods of time when the two direct stimuli are present and, at the same time, there appear (at the time of the army's return) the first manifestations of a directed reaction when the slaves begin to behave appropriately to the situation. And then it becomes evident that those reactions are specific in each of the two studied slave-species. In *F. fusca,* the initially general arousal finds an outlet in the enlarging of the narrow entry holes to the nest (Fig. 5 and 6). *F. cinerea,* on the other hand, more and more frequently and in larger numbers, collect the pupae abandoned on the nest and, in time, begin to take them forcefully away from the returning amazons and carry them to different entry holes (Fig. 2 and 3 *C*). The gathering of prey by the slaves was already described by Huber (9) in 1810, but because of a small number of observations he could not connect those facts with given slaves-species. Beck (1) regarded the leaving of the pupae on the nest's surface by the returning amazons as a normal

phenomenon and it can be therefore inferred that he was dealing with slaves other than *F. fusca.*

The fact that the two slave species have different reactions to stimuli that come from the same source can be explained by biological dissimilarities. A nest which is bulit by slaves in accordance with their biological predispositions is not suited to the mass inportation of prey by the slave-making ants who, in addition, have a tendency to use only one hole — that through which they left. The "traffic-jam" that occurs when the army returns must inevitably arouse excitement in the nestmates. For the *F. cinerea*-slaves, the amazons themselves provide the solution to the problem, since some of them, in nests with those slaves, drop their prey to the ground from the very first raids (Fig. 4, dashed line). On the territory occupied by *F. cinerea* colony, every strange object is immediately removed and the prey is brought inside the nest. Those polycalic ants bring the prey in through all the entry holes, which they make large and numerous, thus liquidating, the "traffic-jam" created by the amazons crowding in one hole. When the slaves' arousal has been directed to carrying the pupae into the nest, and there are no more pupae abandoned on the ground, the slaves being to snatch the pupae away from the mandibles of crowding amazons.

The *F. fusca*-slaves behave differently. Only an experienced forager of this species picks up without hesitation the prey lying on the ground. In the crowd of slave-making ants, an accidentally dropped pupa lies on the ground, sometimes for a long time, trampled by the amazons and the slaves. And it turns out that in those nests the amazons do not drop the pupae neither during the first few nor the subsequent raids, but instead, carrying the pupae, persistently push their way inside the nest through a most often, single, entry hole. Soon, the *F. fusca* begin to react to it in a similar manner, as during the nuptial flight, although the situation is reversed, because the crowd of inhabitants force their way through the narrow opening *inside* the nest. The slaves' reaction consists in cleaning the grated opening to the nest by removing from it the building material. The very fact that *F. fusca* ants solve the problem in circumstances so far from normal for that species, is by itself the evidence of behavioral plasticity. But the process of adaptation does not end at that reaction consistent in a way with the ethology of the species. During the first raids, the enlarging of the hole begins under the influence of a direct stimulation by the crowd of prey-carrying amazons. It can be very soon observed, however, that the return of the first slave-making ant with prey evokes the same reaction, althought the unconditioned stimulus in the form of a crowd in the opening has not yet acted. On the average, from the raid 10 onwards, the departure of the army becomes

a stimulus that evokes an appropriate reaction of the slaves. It was confirmed by the previously described amusing event when a single, aroused amazon-ant inciting to leave the nest, provoked one *F. fusca* worker to remove a single twig from the hole.

Translating the above described phenomena into the language of neurophysiology, the ants' reaction is now evoked by the conditioned stimulus (the army's departure), associated by them with the unconditioned stimulus (the army's return with the prey), which occurs after a break of 25 - 40 min.

The undirected arousal of *F. fusca,* induced by the raids and manifested in agression, subsides when it finds an outlet in the appropriate, conflict-diffusing building activity. An interesting example of displacement activity sporadically observed is covering the hole when the raid does not take place at its usual time. The activated building activity manifests itself here in a different, more natural for this species form. Uncovering the holes and exposing the nest to a possible enemy, so inconsistent with the normal behavior of *F. fusca,* proves to what extent the behavior of those ants, has changed under the influence of cohabitation with the *P. rufescens.*

It should be said that the described and analysed behavior of the slaves does not necessarily constitute a general rule for given *Serviformica* species. The workers, who belong to slave-species, become slaves without being equipped for that role by either inborn patterns of behavior, or individually acquired habits. They live isolated from normal families of their own species that reproduce themselves and they die without progeny. It is quite possible in those conditions that the adaptational changes that occur in individual slave-making ants' nests can be different in various nests, because they are formed in every one of them independently.

It should be noted that the discovered differentiation of behavior among the amazons, dependent on the species of their slaves, contradicts the opinion of their total lack of plasticity. The only mention of certain ethological changes occurring in the amazons under the influence of their slaves was found by us, once again, in Forel (8). According to his observations, the amazons' raid-making season begins earlier if they have *F. rufibarbis* for slaves. Also, their army is then faster and moves in closer order. Forel rejects the supposition of a possible secondary division of *P. rufescens* into different species or varieties that keep different slave species. We can say in support of his opinion that there occur, infrequently, the nests of amazons with slaves belonged to two species. It negates the existence of varieties genetically adjusted to particular slave species.

Wheeler (13) suggests a different interpretation of the example described by Forel. He expresses the opinion that the slave-making ants do not change under the influence of *F. rufibarbis*-slaves, but that they belong to more militant families due to which they are capable of enslaving the highly aggressive *F. rufibarbis.*

The amazons' tendency to abandon the prey and surrender it to the *F. cinerea*-slaves, recorded in this paper, is alone inconsistent with their normal behavior. Tris tendency acquires a special meaning when the structure of *F. cinerea* nest is compared with that of *F. fusca,* where the amazons only sporadically behave in that manner. The wide openings in the *F. cinerea* nests make bringing the prey inside incomparably easier than in the nests of *F. fusca* with their narrow grated holes. The behavior of the amazons, persistently bringing the prey inside through the narrow, frequently single opening to the *F. fusca* nest, but dropping it around the numerous and wide openings to the nest of *F. cinerea,* not only differs depending on the slave-species, but is also *in conflict with the immediate stimuli.* It can be explained by the specific behavior of the slaves themselves, which evokes in the slave-making ants a specific adaptational reaction. It does not, however, explain the phenomenon of abandoning the prey by some amazons already from the first raids of the season. The interpretation which suggests itself here should be undoubtedly verified experimentally. It is highly probable that the habits acquired by old solidiers in the previous year manifest themselves in this case. It should be taken into consideration that the attack, abduction and bringing of pupae are the only functions performed by the amazons' soldiers and that, in the interval between two seasons, they do not perform any social functions, remaining numb after a period of excessive arousal and activity. Such conditions are conducive to the survival of acquired habits, because they are not effaced by new habits and sensations. Young soldiers who go out in a given season for the first time do not have similar habits and act in accordance with the inborn patterns of behavior by taking the prey inside the nest. Very soon, however, the *F. cinerea*-slaves aroused by the pupae dropped by the last year's soldiers begin to wrench the prey away from the arriving amazons, for whom the possibility of an immediate return to the raided nest becomes an additioned positive stimulus. It can be presumed that learning by the imitation of old soldiers who drop the pupae and surrender them to the slaves is the factor which speeds up the acquisition of the new pattern of behavior by the slave-making ants.

The habits which the slaves acquired in the previous year do not have as good conditions for survival as those which are assumed to exist in the case of the slave-making ants. In between the two seasons of

the *P. rufescens*' activity, the slaves lead a normal life, similar to life in the nests free of social parasites. It is not likely that the presence of passive slave-making ants in the nest should have a great influence on the behavior of their slaves. At the most the slaves could be expected to show an increased excitability or aggressiveness under the influence of secretions which they licked off the *P. rufescens*' female, off-spring or soldiers. The increased arousal of the slaves finds an outlet, because the permanent presence in the nest of several thousand individuals who are nonproductive for a substantial part of the summer requires increased efforts for the care and feeding of the community. Besides the slaves probably lead a normal life and are likely to forget the foreign patterns of behavior imposed by the amazon raids, and with each season have to learn them anew. On the other hand, if the above reasoning is correct, the process of learning in the slaves is facilitated by the behavior of last year's amazons, which is now consistent with the reactions of their slaves.

In our opinion, the adaptable behavior of the amazons dependent on the subordinate species of slaves ascertained beyond doubt in this study, as well as the signs of survival of habits acquired in the previous year, prove that the species has the ability to learn. So far, we have found in literature only one mention by Raignier (11), who in the ability of *P. rufescens* female to establish new nests in five different ways, saw the evidence of the plasticity of this species and its ability to adapt itself to new circumstances.

How to reconcile these facts and conclusions with the extensive evidence of the lack of plasticity in *P. rufescens*? The rigid requirement of strictly definite stimuli which evoke strictly definite responses can govern only those behavioral acts which are performed by the slave-making ants alone, without the participation or even the contact with the slaves, i.e., the raids, the abduction of the pupae and bringing them to the nest. However, besides performing that sole social function, the amazons remain members of the community and are dependent on a constant contact with and adjustment to the cohabiting slave species who carry out the remaining social functions. Thus, the ants *P. rufescens*, being parasites, have nevertheless remained social animals. The necessity to coexist and the dependence in all purely social aspects of life on the normal, not degenerated slaves, allows the amazons to retain at least some plasticity of behavior and ability to adjust to specific conditions, common to social animals.

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