

Short communication

Integration raids in the Amazon ant *Polyergus rufescens* (Hymenoptera, Formicidae)

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Summary. Groups of enslaved *Formica fusca* workers from mixed colonies of *Polyergus rufescens* with numerous slave workforce tend to split off and found small and almost hom-specific nests around the main nest, with at least some of them connected with the latter with underground passages. Their inhabitants are able, at least temporarily, to adopt young *F. fusca* gynes. *P. rufescens* invades these satellite nests in a manner similar to the normal slave raids, and carries the slaves back to the main nest. The supposed evolutionary cause of this behaviour is to keep integrity of mixed colonies and prevent possible emancipation of slaves.

Key words: Social parasitism, mixed colonies, colony organisation, slave emancipation, *Formica fusca*.

Introduction

The most frequent slave species of *P. rufescens* in Central Europe is *Formica fusca*, principally a mono- or slightly polygynous and monocalic species. Its workforce usually numbers from several hundred to a thousand, rarely reaching 1,500–2,000 adults in particularly big colonies (Savolainen, 1990; Seifert, 1996). Swarms of *P. rufescens* may number up to about 2,000 workers (see below), and the proportion of slaves in its mixed colonies reaches 80–90% (Seifert, 1996). This means that a *P. rufescens* nest may support between 8,000 and 18,000 enslaved workers, what exceeds several times the common size of a free-living colony of *F. fusca*. Thus, the multiplication of swarm size typical of *F. fusca* caused by *P. rufescens* is a peculiar experiment of nature. The response of *F. fusca* to this situation has revealed a peculiar element of *P. rufescens* biology.

The phenomenon was noticed and investigated during observations of two big colonies of *P. rufescens* mixed with *F. fusca* in the Białowieża Forest (NE Poland) in 2002 and 2003 in the periods of their raiding activity (late July/early August). The raiding columns were estimated to comprise up

to 2,000 workers. Both colonies displayed the behaviour discussed, and it was especially spectacular in one of them.

Observations

The main nest of the mixed colony, inhabited by *P. rufescens* and the majority of the slave swarm, was situated in a low bank, with a few close entrances on its top. At the foot of the bank, several satellite nests were scattered around an area of nearly 5 m². The largest distance between a pair of these satellite nests was 3.2 m, and the distances between individual satellite nests and the holes of the main nest ranged from 1.6 to 4.4 m. At least some of these filial nests were connected with the main one by underground tunnels. The entire arrangement resembled a compound nest system of *F. cinerea* (see e.g. Dlussky, 1967). Satellite nests were small and superficial (in litter, under a stone or a piece of wood), each inhabited by not more than a few dozen *F. fusca* workers. Some of them included small groups of young sexual adults and sexual pupae of *P. rufescens*. Sporadically, single *P. rufescens* workers were seen in the satellite nests, but neither *P. rufescens* worker pupae nor *F. fusca* enslaved pupae could be found there.

The colony exhibited high raiding activity. It often and successfully raided neighbouring *F. fusca* within a 77-metre radius. Apart from usual distant raids, *P. rufescens* performed short-distance raids on their own satellite nests. These peculiar raids took place almost every day during the observation periods (3 weeks each year), even when the weather was not good enough to undertake a long-distance raid. Their organisation was identical to that of typical raids – from the recruitment phase to the outbound column reaching the target nest (see e.g. Mori et al., 1991). The difference appeared when the “attackers” met the *F. fusca* workers, which were, in fact, their colony mates. The ants would establish contact in a friendly manner, palpating each other with antennae, which was mainly initiated by *F. fusca*, noticeably astonished (but not frightened) at that sudden inroad. The excitement of

P. rufescens workers would decline from that moment and the majority of them would start to withdraw, with only a small group entering the “raided” nest. After a few minutes, these individuals would go back towards the surface, carrying *F. fusca* adults in their mandibles, and join the end of the inbound column. In about 90% of cases, a carried slave was seized by the mandible or by the antenna base, and it took on the typical posture for adult transport in *Formica* species. The rest were taken hold of in every possible way (by the pedicel, leg or antenna) and dragged along on the ground, never attempting to free themselves.

There would be several such peculiar raids in one day, their subsequent waning waves gradually merging with one another, so that initially well organised raids would transform into permanent individual activity of *P. rufescens* workers. Usually, in the meantime, the main forces would make an ordinary raid to a foreign *F. fusca* colony. Adult transport of slaves from the satellite nests until dusk, i.e. 3–4 hours. Its average efficiency was about a dozen of individuals/min. (max about 30), which corresponds to 2–3 thousand slaves carried from one or a few (very small) nests of the main nest daily. The only reliable explanation for such intensity of transport is that the transferred individuals came back immediately or that they were being systematically replaced by an influx of other workers to satellite nests from the main nest through underground passages (there was no increased *F. fusca* on the surface). It is also thinkable that the “attackers” used these passages to reach their own nest and obtained their “victims” from there. If so, however, one could expect that they would walk off with enslaved pupae rather than with adult slaves.

During the observations, nuptial flights from neighbouring free-living *F. fusca* colonies were going on, and young gynes were seen on the ground now and then. Twice in 2002, *F. fusca* gynes, apparently – at least temporarily – adopted by enslaved *F. fusca* workers, were noticed in satellite nests of the mixed colony. On 1st August, one such nest was dug up, and a *F. fusca* microgyne was found inside. Unfortunately, it was fatally wounded during the inspection. This nest was 3.2 m away from the entrances of the main nest and it was connected with the latter by an underground passage. Then, on 3rd August, a *F. fusca* macrogyne was seen for a while under a stone covering another satellite nest, 3 m away from the main nest entrances. It was accompanied by a dozen or so of *F. fusca* workers; immediately after the nest was uncovered, the gyne hid inside the ground. Its further fate is unknown.

Discussion

The questions arise about the mechanisms underlying the behaviour reported (proximate factors) and its biological sense (ultimate factors). Regarding the mechanisms, two

opposing hypotheses concerning the discriminative abilities of *P. rufescens* come to mind. The first holds that there are some slight differences between the odour signatures of *F. fusca* workers from the main nest and those from the satellite nests, and that *P. rufescens* is able to detect these nuances. The first of these assumptions, however, seems to be hardly probable, because of constant intense circulation of *F. fusca*, caused by *P. rufescens* itself. The second hypothesis is that *P. rufescens* does not distinguish its own, enslaved individuals from foreign, “free” ones of the same species, and that it is ready to attack each nest of a dulotic species within its range when the automated sequence of raid phases is completed, including a march (even the shortest) of the organised column. If the target is their own satellite nest, the attackers, fulfilling their robbery instinct, catch and take *F. fusca* workers out, since there are no pupae and adults passively submit themselves to it, with no resistance. This fits well the old conjecture of Dobrzański and Dobrzańska (1978) that the dulotic instinct of *P. rufescens* is directed not only at pupae but (potentially) also at mature workers of slave species.

The biological sense of the described *P. rufescens* behaviour may lie in preventing disintegration of mixed colonies by split-offs of slave groups and their possible emancipation due to conspecific queen adoption. Some observations (Czechowski, unpubl.) suggest that such emancipation actually happens under certain environmental conditions. With *P. rufescens* not counteracting this process, nests of the former slaves might eventually surround its colony in a tight competitive circle.

These ‘integration’ raids of European *P. rufescens* are the second kind of intracolony raids known in this genus. Earlier, so called ‘emigration’ raids were described in North American *P. lucidus* by Kwait and Topoff (1983). It may be assumed, that the general mechanisms of both phenomena are the same.

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