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Research note

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THE ROUTE OF *FORMICA POLYCTENA* FÖRST. AS A FACTOR  
PROMOTING EMANCIPATION OF *FORMICA FUSCA* L.  
SLAVES FROM COLONIES OF *POLYERGUS RUFESCENS* (LATR.)  
(HYMENOPTERA: FORMICIDAE)

**ABSTRACT:** *Formica fusca* L. slaves from colonies of *Polyergus rufescens* (Latr.) tend to establish small homospecific satellite nests close to a main nest. *P. rufescens* maintains the integrity of a mixed colony by means of peculiar integration raids (Czechowski 2005). The present paper describes the history of a group of such satellite nests, temporarily separated from the main nest by a foraging route of *Formica polyctena* Först. impassable to *P. rufescens*. The ex-slaves had managed to adopt *F. fusca* gynes and raised some homospecific worker pupae before the *F. polyctena* route disappeared and *P. rufescens* started to raid their nests. During the raids, the mutual attitude of the slave-makers and the ex-slaves quickly evolved from hostility to friendly relations.

**KEY WORDS:** ants, social parasitism, slavery, mixed colonies, interspecific relations

Groups of *Formica fusca* L. slaves from mixed colonies of *Polyergus rufescens* (Latr.), an obligatory slave-maker, with numerous slave workforce tend to split off and establish small, almost homospecific nests in the vicinity of the main nest. *F. fusca* workers from these satellite nests are able, at least temporarily, to adopt young conspecific gynes. *P. rufescens* invade such satellite nests in a manner similar to their normal slave raids,

and carry the slaves (adults) back to the main nest. The supposed evolutionary cause of these peculiar intracolony integration raids is to maintain unity of a mixed colony and prevent possible emancipation of slaves (Czechowski 2005).

There is evidence to show, however, that such emancipation actually occurs under certain environmental conditions. This phenomenon was observed in the same *P. rufescens* + *F. fusca* colony that was described when reporting integration raids. The study was conducted in the Białowieża Forest (NE Poland) in 2002 and 2003 from mid-July till mid-August, i.e. in the period of *P. rufescens* raiding activity.

The colony of *P. rufescens*, with a high percentage of *F. fusca* slaves, nested within a territory of wood ants, *Formica polyctena* Först., at a distance of 7.5 m from a nest of the latter. The mean dynamic density of wood ants dispersed around the *P. rufescens* nest, in its nearest vicinity, was  $15.5 \pm 5.2$  ind.  $\times 0.25 \text{ m}^2 \times 5 \text{ min}^{-1}$  ( $n = 6$ ). In 2002 a *F. polyctena* foraging route 1.5 m wide ran 1 m to the north of the *P. rufescens* nest in a south-east to north-west direction (Fig. 1). The mean dynamic density of *F. polyctena* workers within the route was  $766 \pm 42$  ind.  $\times 0.25 \text{ m}^2 \times 5 \text{ min}^{-1}$  ( $n = 5$ ). The route was not

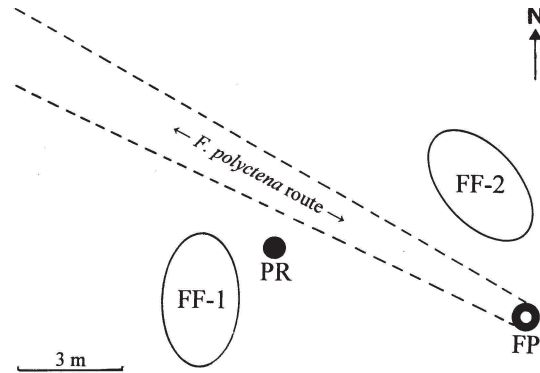


Fig. 1. Scheme of the situation of the studied nests and nest complexes: PR – main nest of *P. rufescens* + *F. fusca* mixed colony, FF-1 – complex of small, almost homospecific, *F. fusca* nests permanently raided by *P. rufescens* in 2002 and 2003 (integration raids; see Czechowski 2005), FF-2 – complex of small autonomous *F. fusca* nests raided by *P. rufescens* in 2003 (when *F. polyctena* route disappeared), FP – nest of *F. polyctena*.

impassable for the enslaved *F. fusca* workers, which were able to sneak among wood ants but it was entirely impassable for *P. rufescens* – both for single scouts and for raiding columns. *P. rufescens* did not even try to move in that direction. Once, when a recruitment circle of *P. rufescens* moved to the wood ant route too close, *F. polyctena* fiercely attacked the outermost individuals and killed about ten of them with no response of the rest of the *P. rufescens* swarm.

All raids that year, including short-distance (1.6–4.4 m) integration raids to satellite nests (Fig. 1) (see Czechowski 2005), were made in other directions, mainly to the south and south-west. Normal, long-distance slave raids ranged from 14 to 30 m. In the next season (in 2003), the foraging route of *F. polyctena* disappeared, enabling *P. rufescens* to carry out east- and northbound raids. That year, besides typical slave raids, ranging from 15 to 77 m, and typical integration raids, one could observe a third type of raids, intermediate in terms of distance to targets, raid recurrence, the course of conflicts and mutual attitude of attacking and attacked ants. Their aim was a group of small, cryptic *F. fusca* nests, situated to the east of the *P. rufescens* nest, just behind the former *F. polyctena* route. These nests were scattered around an area of about 8 m<sup>2</sup>. The largest distance between a pair of these nests was 1.8 m, and the distances between individual nests raided and the nest of *P. rufescens* ranged from 5.3 to 7.1 m. The complex included at least six such *F. fusca*

nests, noticed to be raided (some of them twice) by *P. rufescens* (Fig. 1).

In 2003, the area inhabited by these small *F. fusca* colonies was intensely searched by enslaved *F. fusca* workers, most of them running distinctly in this direction on leaving the *P. rufescens* nest. Besides regular, individual searching activity, they organised peculiar raid-like expeditions. From time to time, groupings of a few to about 20 individuals left the nest and decidedly, in a loose column, made their way straight towards the homospecific *F. fusca* nest area. On reaching the place, the ants would disperse, and thus the assignment of these peculiar raids of slaves remains unclear. In any case, they were not connected with the raiding activity of their host, *P. rufescens*. The same behaviour of slaves was observed by the author at another *P. rufescens* colony in the Białowieża Forest which also carried out integration raids.

The course of raids on the *F. fusca* nests under discussion was identical to that of regular *P. rufescens* raids (see e.g. Mori et al. 1991, Le Moli et al. 1994) – from a recruitment phase to robbery of pupae, if they were present in the attacked nest. The spoils of these raids were very scanty, if any. *P. rufescens* raided this area 11 times from 5<sup>th</sup> to 16<sup>th</sup> August; before that period it organised only long-distance (very successful) slave raids and short-distance integration raids. Altogether, these middle-distance raids provided *P. rufescens* with less than 200 *F. fusca* worker pupae and last instar larvae. A *F. fusca* queen

escaped from one of the nests attacked. Nests were sometimes raided again on the same or another day irrespective of the presence or absence of a booty. The difference between this type of raids and typical slave raids was visible in the final stage of the former, when a substantial part of the *P. rufescens* swarm tended to prolong their stay at the *F. fusca* nest, with single workers found even inside the nest on the following day. The initial mutual aggressiveness of the attacked and attacking ants gradually declined and evolved into apparently friendly relations (palpating each other with antennae). At the same time, *P. rufescens* began to try, with more or less success, to transport *F. fusca* adults (fully coloured and able-bodied workers) to its own nest in the same manner as during integration raids (see Czechowski 2005). *P. rufescens* either took *F. fusca* workers out of the interior of the nest or simply picked them from among individuals that tried to block the nest entrance. However, the efficiency of adult transport was incomparably lower than during integration raids because of much less involvement of *P. rufescens* in this task, as well as much lower susceptibility of *F. fusca*. Altogether, during the observations not more than 50 *F. fusca* adult workers from the nests under discussion were transported to the *P. rufescens* nest in this way. Interestingly, during prolonged mutual interspecific palpating it was *P. rufescens* individuals that were closer to taking on the submissive posture.

In view of the circumstances presented here and in a previous paper (Czechowski 2005), the colonies of *F. fusca* under discussion, raided by *P. rufescens* in a peculiar way, appear to have originally derived from the colony of the latter. In other words, they seem to be colonies of successfully emancipated slaves which had managed to break away from the mixed colony, adopt their conspecific queens (at least some of them) and had become fully independent and autonomous. They owed this opportunity to a lucky coincidence – the neighbourhood of a colony of wood ants and their foraging route right next to the social parasite nest. Unlike *P. rufescens*, *F. fusca* individuals were able to cross the *F. polyctena* route quite freely due to the opportunistic character of this submissive species (see e.g. Savolainen and Vepsäläinen

1989, Savolainen 1990). Most apparently, groups of them founded some small, necessarily homospecific, satellite nests behind the route, in the area inaccessible to *P. rufescens*. In that situation, the mechanism of *P. rufescens* serving to maintain integrity in mixed colonies preventing slave emancipation, i.e. integration raids (Czechowski 2005), could not work. The initial hostility between former heterospecific nestmates was caused by their long, at least one-year, separation. In respect of possible transfer of colony odour, the separation was not absolute as enslaved *F. fusca* workers continually (except for the winter break) contacted ex-slaves in their nest area, and maybe even in their nests. The quick disappearance of mutual hostility might actually have been due to this 'buffer' effect of slaves.

This contribution, together with the previous one (Czechowski 2005), give a complete description of the raiding behaviour utilised by *P. rufescens* for preventing emancipation of slaves, as well as they strongly suggest that such emancipation is not only a potential threat to *P. rufescens* colonies, but it really happens under certain environmental conditions, like, for example, the circumstances presented above. Of course, in this particular case, it is hard to discern any evolutionary strategy of *F. fusca* slaves, a strategy that would favour the use of wood ants' foraging routes as a mechanism to achieve emancipation. It was a strange coincidence rather than a sign of the evolutionary established strategy.

There are no doubt, however, that the integration raids described earlier (Czechowski 2005) express evolutionary strategy of *P. rufescens* to keep integrity of mixed colonies and prevent possible emancipation of slaves. The finding presented in this note, i.e. reality of the threat of slave emancipation, confirms the previously suggested ecological context of the biological sense of integration behaviour: with *P. rufescens* not counteracting slave emancipation, colonies of the ex-slaves might eventually surround the social parasite colony in a tight competitive circle (Czechowski 2005).

The very mechanisms of supposed emancipation of *F. fusca* slaves from colonies of *P. rufescens* in the reported case resembles

those of indirect protection of slave species nests (*F. fusca*, *F. cinerea* Mayr) against raids of *Formica sanguinea* Latr., another slave-maker, given by territorial ants [*Lasius fuliginosus* (Latr.), *Formica rufa* L.] (see Czechowski 1999, 2000, Czechowski and Vepsäläinen 2001). The phenomenon of slave emancipation as such has only been reported to date in colonies of *F. sanguinea* mixed with wood ant workers as its atypical slaves. The slaves got rid of the *F. sanguinea* swarm, adopted their conspecific queens and took over the nest (Marikovsky 1963, Czechowski 1996).

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