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Short research contribution

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DO *POLYERGUS RUFESCENS* (LATR.) AND *FORMICA SANGUINEA* LATR. (HYMENOPTERA: FORMICIDAE) SHARE RESOURCES OF SLAVE SPECIES WITH EACH OTHER?

ABSTRACT: The paper discusses the directionality of slave raids of a colony of *Polyergus rufescens* (Latr.), an obligate European slave-making ant species, in the presence of colonies of *Formica sanguinea* Latr., a facultative slave-maker, in the neighbourhood. Both these social parasites use the same host species. The results strongly suggest that *P. rufescens* avoided raiding the area occupied by its competitor. An explanation is offered based on a demonstrated at the same time tendency of this species to avoid dangerous places.

KEY WORDS: ants, social parasitism, slavery, interspecific relations, competition, territoriality

The genus *Polyergus* Latr. and the subgenus *Raptiformica* For. (= *Formica sanguinea* group) contain socially parasitic ant species that are obligate or facultative slave-makers, respectively. *Polyergus* includes five species (3 Palaearctic, 2 Nearctic) compared to thirteen species (1 Palaearctic, 12 Nearctic) in *Raptiformica*. In Europe, these taxa are represented by one species each: *Polyergus rufescens* (Latr.) and *Formica sanguinea* Latr. While the habitat niches of these species partly overlap – the former is an oligotope of

dry grasslands and the latter is a polytope of dry habitats – they rarely co-occur because *P. rufescens* is, at least in Central Europe, a rare species. Its rarity is actually the reason why nothing is known about their mutual relations, which are worthy of interest as both the slave-makers raid and enslave the same host species, members of the subgenus *Serviformica* For. (see e.g. Mori *et al.* 2001). Therefore severe interspecific competition between them, even of the contest type, can be expected, especially as intraspecific raids are known to launch both in *P. rufescens* (Dobrzańska 1978, Le Moli *et al.* 1993, Grasso *et al.* 1994, Mori *et al.* 2001) and *F. sanguinea* (Czechowski 1990), and those in *P. rufescens* are interpreted as signs of intraspecific territorial competition (Grasso *et al.* 1994, Mori *et al.* 2001).

Interactions between *Polyergus* and *Raptiformica* ants are hardly known in general. To date only Bono *et al.* (2006) have paid attention to this issue in their research on the raiding activities of the North American slave-maker *Polyergus breviceps* Em. versus those of *Formica puberula* Em. and *F. gyncrates* Snelling et Bure against their common slave species, *Formica occulta* Francouer and *F. argentea* Wheeler. Their results have

shown that colonies of those slave-makers seemed to avoid raiding areas exploited by another colony both in intra- and interspecific relations. Mori *et al.* (2000) noted the same with regard to intraspecific relations in the European *F. sanguinea*.

The present contribution reports observations which suggest that the same is true of interspecific relations between two European slave-makers, *P. rufescens* and *F. sanguinea*. The observations were made when the raiding behaviour of *P. rufescens* and relations between the latter and the wood ant *Formica polyctena* Först. were investigated in Białowieża Forest (NE Poland) in the years 2001–2003 in the periods of *P. rufescens* raiding activity (see Czechowski 2005, 2006, 2007).

One of two big *P. rufescens* colonies studied there, PR-I, inhabited a neglected coniferous-deciduous forest plantation occupied by two territorial ant species, *F. polyctena* and *F. sanguinea* (for hierarchical organisation of ant assemblages see Vepsäläinen and Pisarski 1982, Savolainen and Vepsäläinen 1988, Pisarski and Vepsäläinen 1989). The whole area of the habitat was strewn with nests of *F. fusca*, an opportunistic submissive ant that was the slave species both for the *P. rufescens* and the local *F. sanguinea* colonies. PR-I nested within the marginal part of the *F. polyctena* territory, but its raids often entered the intensively searched part of the wood ants' territory. The route of the most distant successful raid on a *F. fusca* nest was 55 m long (see Czechowski and Markó 2006), and the longest in general, but failed raid reached 56 m. Four colonies of *F. sanguinea* were situated within this radius from the *P. rufescens* nest (15–47 m from PR-I; Fig. 1). During the three seasons, a total of 23 raid routes and ca. 30 raids (some targets were raided more than once) were registered. Thirteen *F. fusca* nests, four *F. polyctena* nests (see Czechowski 2007) and one unidentified empty nest were subjected to raiding; five raids were broken off without reaching their goals. Most raids against *F. fusca* nests were directed west of PR-I, towards a strip of open area between patches of thicket, and, at the same time, towards the centre of the *F. polyctena* territory. No raids targeted the interior of a very dense and dark young cop-

pice to the north, which was understandable as there were practically no host colonies there. No raids were also made to the south, entering the territory of *F. sanguinea*, which occupied a vast area of habitat identical to that raided by *P. rufescens* in the west. What is more, the only two raids directed that way stopped and failed, having covered distances of only 7.5 and 9.6 m, respectively, despite no evident problems related to weather or time (Fig. 1).

It is true that in areas under threat from *F. sanguinea*, the abundance of *F. fusca* is higher within than outside territories of wood ants (Czechowski and Vepsäläinen 2001). That was also the case in the habitat studied (see Czechowski and Markó 2006). However, it seems hardly probable that the *F. polyctena* territory would be so attractive in that respect for *P. rufescens* as to completely prevent the latter from exploiting the potential slave resources on the remaining (bigger) part of the area habitable for *F. fusca*, the more so as some raids were also directed to the east, i.e. in the opposite direction to those exploring the territory of *F. polyctena*, but also not intruding the territory of *F. sanguinea* (Fig. 1). Such a pattern of distribution of *P. rufescens* PR-I raids strongly suggested that that colony avoided raiding the area used by *F. sanguinea*, especially in the light of Bono's *et al.* (2006) analogous findings for the North-American slave-making species.

As for the possible origin of *Polyergus* avoidance of raiding *Raptiformica* territories, Bono *et al.* (2006) assumed that the avoided areas had been established by *Polyergus* scouts involving olfactory cues. Most probably, however, the avoidance is a response to previous dramatic experiences of a given slave-maker colony.

Despite a tendency for spatial distribution of raiding, there are occasional intraspecific raids in both *Raptiformica* (at least in *F. sanguinea*; Czechowski 1990) and *Polyergus* (both North-American and European species; Talbot 1967, Marlin 1969, Dobrzańska 1978, Topoff *et al.* 1984, Le Moli *et al.* 1993, Grasso *et al.* 1994, Mori *et al.* 2001, Bono *et al.* 2006), as well as interspecific raids of one slave-maker against another (at least *F. puberula* vs. *P. breviceps*; Bono *et al.* 2006). What is more, foreign

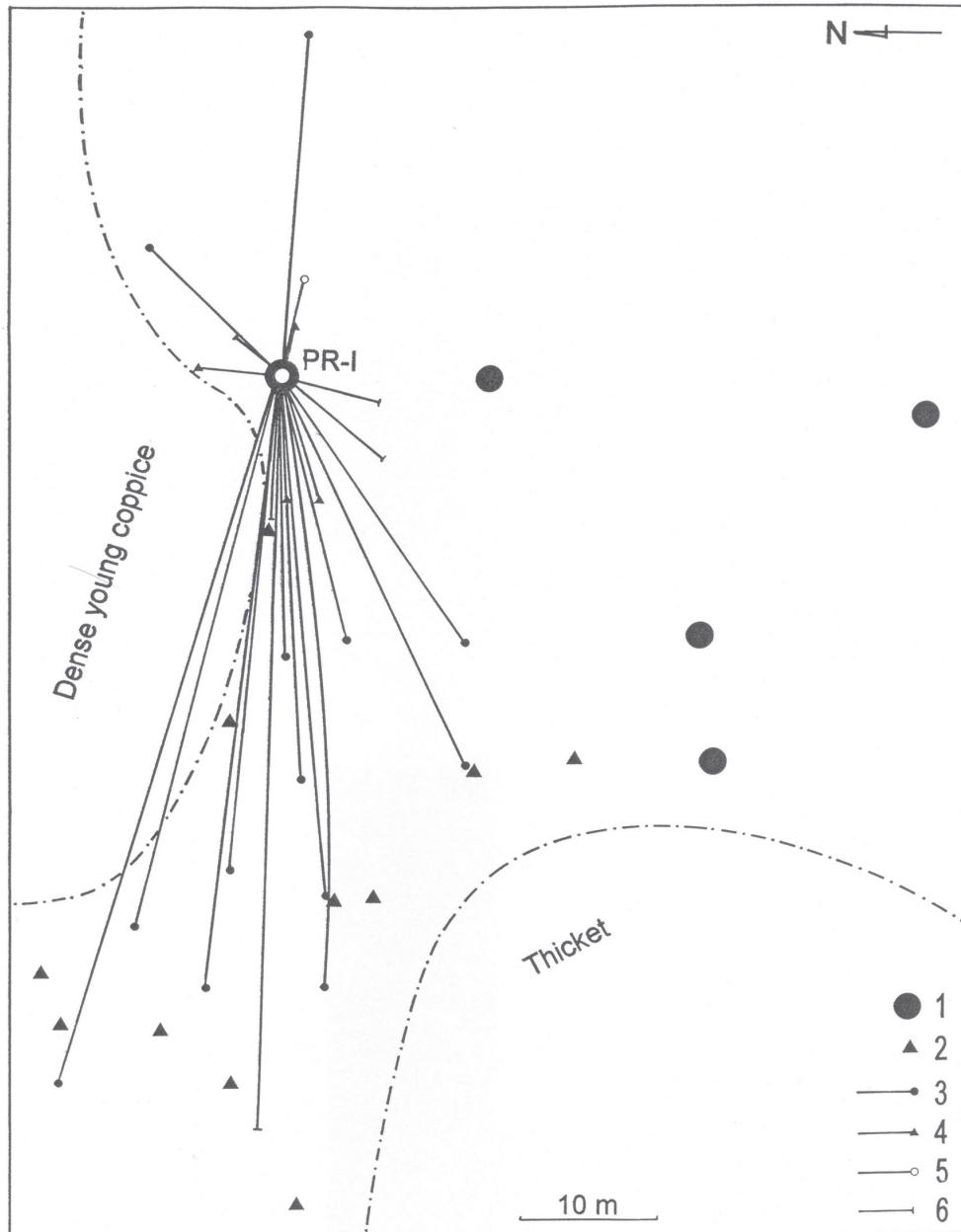


Fig. 1. Directionality of the raids of *P. rufescens* PR-I against a background of the distribution of *F. sanguinea* and *F. polystena* colonies in the neighbourhood (1 – *F. sanguinea* nest, 2 – *F. polystena* permanent nest, 3–5 – raids targeted to: 3 – *F. fusca* nest, 4 – *F. polystena* small nest, 5 – unidentified abandoned nest, 6 – failed raid (without reaching a target).

raiding columns sometimes encounter each other on their routes (*P. breviceps* vs. *P. breviceps* and *P. breviceps* vs. *F. puberula*; Bono *et al.* 2006, *F. sanguinea* vs. *F. sanguinea*; W. Czechowski – unpublished). Such situations usually lead to fierce combat and considerable losses on both sides (see the above references).

On the other hand, certain observations by the author made while studying the raiding behaviour of *P. rufescens* in Białowieża Forest (see above) revealed that *P. rufescens* were able to imprint dangerous places in the colony's memory and subsequently avoid them. There was a zone impassable for *P. rufescens* (scouts, pre-raid 'circlers' and columns)

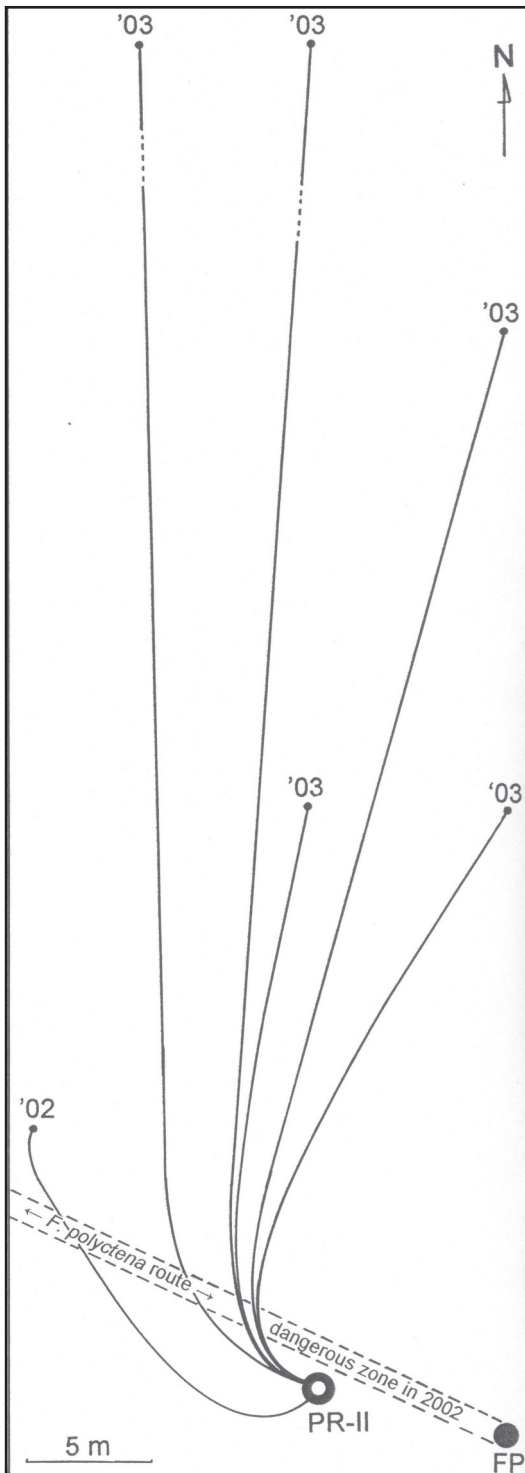


Fig. 2. Routes of the raids of *P. rufescens* PR-II directed beyond the functioning (in 2002) and extinct (in 2003) *F. polycytena* foraging route (FP – *F. polycytena* nest).

and not passed by them, namely a part of the *F. polycytena* foraging route, that ran 1 m to the north *P. rufescens* PR-II nest. That part was impassable due to an extremely aggressive attitude of *F. polycytena* within that very section of the route (see Czechowski 2006, 2007). In 2002, when the *F. polycytena* foraging route was in operation, only one raid was directed to *F. fusca* nests beyond the route, at a distance of 15 m from PR-II. To reach its target, the raiding column of *P. rufescens*, steering clear of the dangerous section, took considerably roundabout routes to pass the *F. polycytena* foraging route in a relatively safe place (see Czechowski 2007), forcing the column to cover a distance 4 m longer (ca. 27%) than the shortest possible one (Fig. 2).

An even more interesting fact clearly in support of the hypothesis on the role of the *P. rufescens* colony memory in its avoidance of dangerous areas is that the detour was taken again the following year, when the *F. polycytena* route had already disappeared and the passage to northerly directed raids was open. Several such raids were observed (20–77 m long) and each of them began with an arched bypass of, the already non-existent dangerous section of the former *F. polycytena* foraging route (Fig. 2).

As regards the *F. sanguinea* colonies sharing the habitat with *P. rufescens* PR-I, their raiding activities were not the object of observation. Anyway, no raids of *F. sanguinea* ants were seen in the area exploited by *P. rufescens*.

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