

INTERFERENCE OF TERRITORIAL ANT SPECIES IN THE COURSE OF RAIDS OF *FORMICA SANGUINEA* LATR. (HYMENOPTERA, FORMICIDAE)

WOJCIECH CZECHOWSKI

Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00-679 Warszawa, Poland,
e-mail: wez@robal.miiz.waw.pl

Abstract.— The paper presents four cases of territorial ant colonies interfering in the course of *Formica sanguinea* Latr. raids against slave species which nest next to or in their territories. In three cases, *Formica rufa* L., when protecting its own territory, forced out (one case) or held (two cases) a raiding column of *F. sanguinea*, thus “saving” local *Formica fusca* L. nests from danger. In one case, *Lasius fuliginosus* (Latr.) did not let a *F. sanguinea* column pass its territory; to reach its target (a colony of *Formica cinerea* Mayr), the column had to by-pass the foreign territory.



Key words.— ants, *Formica sanguinea*, *Formica rufa*, *Formica fusca*, *Formica cinerea*, *Lasius fuliginosus*, territoriality, competition, slavery, ecology.

INTRODUCTION

Ant assemblages have a hierarchic structure. They are dominated by territorial species, that defend their foraging areas (territories) (Pisarski 1973, 1982, Vepsäläinen and Pisarski 1982, Savolainen and Vepsäläinen 1988). Nests of territorial ants form centres of spatial organization of local assemblages (Savolainen and Vepsäläinen 1988, Savolainen et al. 1989). Subordinate (non-territorial) ant species may live in a dominant's territory, but their abundance there is smaller (Punttila et al. 1991), foraging activity reduced, reproductive potential lower, and they may nest only at a certain distance from the dominant's colony, a distance determined by factors affecting its social organization (Pisarski and Vepsäläinen 1989). The relations between *Formica polyctena* Först. (dominant species) and *F. fusca* L. (subordinate species) perfectly reveal the essence of the matter (see Savolainen 1990, 1991).

Under certain conditions, however, the proximity of a stronger partner appears to be advantageous to subordinate species. As Punttila et al. (1996) have found, competition between wood ants of the *Formica rufa* group and *F. sanguinea* Latr. has an indirect effect on the distribution and abundance of the slave species (*F. fusca* and *F. lemani* Bondr.). Recently, I described – beneficial to colonies of *F. cinerea cinerea* Mayr and *F. fusca* – direct interference of *Lasius fuliginosus* (Latr.) (the dominant of the local assemblage) in the course of *F. sanguinea* raids (see Czechowski 1999). In the present paper, I describe further facts illustrating the role of territorial species in stabilizing multi-species ant assemblages.

STUDY AREA AND SPECIES

The observations were carried out in early July 1999 in a complex of sandy dunes gradually overgrowing with pine forest near Tvärminne in southern Finland. Early July is usually the time when *Formica sanguinea* conducts its slave raids there. In addition to *F. sanguinea*, the following species took part in the events described: *F. rufa* L., *Lasius fuliginosus*, *F. fusca* and *F. cinerea cinerea*.

F. (Raptiformica) sanguinea nests in successional forest habitats. It is a facultative slave-maker that raids species of the subgenus *Serviformica* For. They are aggressive ants and during their raiding period they do not respect the boundaries of other species' territories. In the study area, *F. sanguinea* nests were distributed mostly along the edge of sand dunes and the pine forest or a little below the edge.

F. (Formica) rufa nests mainly in mature coniferous forests and also enters mixed and deciduous forests. It is a territorial species. In the study area, monocalic colonies of *F. rufa* (and of other wood ants) nested in the forest, mostly at the foot of the dune belt.

L. (Dendrolasius) fuliginosus is a dendrophile and oligotope of stable deciduous forests which also enters mixed and coniferous forests. It is a territorial species. A colony nesting in a small forest patch on the dune slope was the subject of the present observations and of earlier ones (see Czechowski 1999).

F. (Serviformica) fusca is a eurytopic (ubiquitous) species. These non-aggressive and non-territorial ants are the most frequent slave species of *F. sanguinea* and hosts to temporary socially parasitic wood ant species.

F. (Serviformica) cinerea is an oligotope of dry habitats (wooded and open ones). These are aggressive, territorial ants that generally form vast polydomous nest systems. The species is also enslaved by *F. sanguinea* (see Czechowski and Rotkiewicz 1997). In the study area, these ants were typical for early phases of succession, and ones that nested even in sheer sand.

OBSERVATIONS

I observed four times that a colony of a territorial species clearly exerted influence on the course (and partly on the results) of *F. sanguinea* raids. In three cases, *F. rufa* interfered when *F. sanguinea* attacked *F. fusca* colonies within its territory. In one case, *L. fuliginosus* hindered a column of slave-making ants from passing through its territory. The column was heading for a nest complex of *F. cinerea* situated behind the *L. fuliginosus* territory. The details are given below.

On 1 July, *F. sanguinea* (nesting on the dune slope in a tuft of heather) attacked a *F. fusca* nest situated 18 m away. The nest was located on the forest edge, merely 3.5 m from a small (\varnothing 45 cm, h 40 cm) mound of *F. rufa*. The presence of wood ant foragers on young aspens growing round the *F. fusca* nest indicated that the nest was within the territory of a *F. rufa* colony. The raid was first noticed at about 19 hours when it still was at the initial stage. An hour later, it was intensive; *F. sanguinea* workers had taken over the entire *F. fusca* nest area (about 0.25 m²) and they were beginning to carry home captured *F. fusca* pupae (very rarely) and dead *F. fusca* ants. *F. rufa* reacted to this by forming a dense cordon in the foreground of the conflict close to their nest. The cordon was 30–40 cm long and consisted of several dozen workers. In 30 min, the cordon moved about 30 cm, reached the middle of the nest territory of *F. fusca* and ousted *F. sanguinea* from there. Both sides clearly avoided confrontation and direct encounters between them were rare. At the same time, *F. sanguinea*, robbed freely pupae from the part of the *F. fusca* nest that was not protected by *F. rufa*.

The observations were stopped at about 20 hours but continued on the following morning. The entire nest area of *F. fusca* was then occupied and densely penetrated by over 100 *F. rufa* workers. *F. fusca* did not reveal its presence. *F. sanguinea* ants were dispersed and kept at a distance (about 1 m). They were busy carrying corpses, this time of their own nestmates, from the battlefield to the nest. This suggested that *F. sanguinea* had fought with *F. rufa* because *F. fusca* could not be suspected to cause noticeable losses among the attackers. *F. sanguinea* withdrew completely during that day and conducted no raid till the end of the observations (9 July).



Figure 1. Dune habitat at Tvärminne – the area of the *F. rufa*-*F. sanguinea*-*F. fusca* conflict. The arrow indicates the place of a (big) mound of *F. rufa* on the edge of the forest. Between the forest and an open dune there is a moss-covered ecotone belt settled by *F. fusca*. Nests of *F. sanguinea* are situated on the upper edge of the dune on the left and inlying (photo W. Czechowski).

Two more conflicts observed between *F. rufa* and *F. sanguinea* took place on a much larger scale. In these, a big *F. rufa* colony (the mound was \varnothing 150 cm, h 50 cm) nesting on the forest edge below the dune, and two *F. sanguinea* colonies, that nested on the upper edge of the dune, 90 m from each other, competed. The territory of wood ants comprised a patch of forest and a fragment of a treeless ecotone belt where the sand was covered with a layer of low moss (Fig. 1). Under the moss, numerous nests of *F. fusca* were dispersed.

On the morning of 5 July, one of the *F. sanguinea* colonies, 80 m from the *F. rufa* mound, started a raid towards the ecotone. The ants had traversed the wide zone of sand, reached their target and started plundering the colonies of *F. fusca*. In this way, moving from one *F. fusca* nest to another, *F. sanguinea* covered an area of about 50 m² seizing a huge number of pupae, and at about 14 hours reached an area controlled by *F. rufa*. Wood ant workers formed, 17 m from the mound, an arched, 10 m long mobile cordon along the boundary of the territory. Although not dense (individuals were dispersed every dozen or so cm), the cordon proved impassable for *F. sanguinea*. However, *F. fusca*, fleeing with their pupae from the danger zone, passed through the cordon freely. No encounters between *F. sanguinea* and *F. rufa* were observed but along the route of the raid there were seen maimed blood-red ants returning to their nest, some with their gasters cut off. *F. fusca* could not have caused such injuries.

The raid of *F. sanguinea* lasted until the evening. Throughout the time, *F. rufa* maintained its cordon which divided the ecotone belt and the *F. fusca* population living there into two parts: one left a prey to *F. sanguinea* and the other effectively protected by the colony of the territorial species.



Figure 2. Patch of forest on the dune slope occupied by the *L. fuliginosus* colony. The photograph was taken from the direction of the *F. sanguinea* nest. The route of the raid ran along the right edge of the territory of *L. fuliginosus* which was identical with the area covered with litter. The nest complex of *F. cinerea*, the target of the raid, is on the top of the dune in the central-left part of the picture (photo W. Czechowski).

On the following day, another *F. sanguinea* colony, living over 60 m from the mound of *F. rufa*, repeated the same scenario and invaded *F. fusca* colonies in the ecotone from the opposite direction. This time, the cordon made by wood ants was 8–10 m from their nest, it was 8 m long and as effective as the previous one.

On 6 July, yet another *F. sanguinea* raid was observed, but this one was interfered with by *L. fuliginosus* that nested in a forest „islet“ on the dune slope (see Czechowski 1999). This raid had been preceded (on 3 and 4 July) by *F. sanguinea*'s two failed attempts to pass through the *L. fuliginosus* colony. These raiding attempts were abandoned at the very beginning after the raiders had come up against a cordon of *L. fuliginosus* posted on the boundary (Fig. 2). Before that, single *F. sanguinea* scouts had moved over the alien territory freely, which was possible because in *L. fuliginosus* dispersed penetration is very poor and, in that particular case, most routes ran in tunnels (see Czechowski 1999).

In the end, the raid aiming at a *F. cinerea* colony was conducted along a route bypassing the territory of *L. fuliginosus*. In a straight line through the territory, the *F. cinerea* colony was about 50 m from the *F. sanguinea* nest but the route was 60 m long. That route was also more difficult because it ran steeply upwards on dry, loose sand instead of on compact moss and litter covering the territory of *L. fuliginosus* (Fig. 2).

The raid began at about 14 hours. At 18.00, after a fierce battle with *F. cinerea* (as is usual during a conflict between these species; see Czechowski 1975, 1977) the *F. sanguinea* ants managed to conquer superficially (see Czechowski and Rotkiewicz 1997) the *F. sanguinea* nest complex. After yet another hour, they started to pull pupae of sexuals out to the

ground surface and then dragged them with great difficulty to their nest (these pupae were the only loot of *F. sanguinea*). It was a characteristic feature of this raid that throughout its course a considerable proportion (about 50%) of *F. sanguinea* workers returning to their nest carried a conspecific individual. Individuals “destined” to be carried were collected by their carriers directly from the battlefield or, later, pulled out of the seized nest.

The route which had been used by *F. sanguinea* was the shortest of all possible ones that bypassed the territory of *L. fuliginosus*. A considerable fragment of it (about 20 m) ran along the very edge of the boundary (Fig. 3). Throughout the two-day raid, the other side of the boundary along this semicircular part was densely lined with *L. fuliginosus* ants which prevented the *F. sanguinea* column from taking any short-cut.

The attacked nest system of *F. cinerea* was situated 9 m from the edge of the *L. fuliginosus* territory. During the first day of the conflict (the raid was repeated, but less intensively, on the following day), some *F. sanguinea* workers tried to return to their nest not by the shortest route possible. They headed straight for the foreign territory, but there they were stopped by a loose cordon of *L. fuliginosus* (Fig. 3). The *F. sanguinea* workers, without trying to push their way through, turned back to the area of the conflict with *F. cinerea* (about 10 m steeply up and along dry sand) and there they joined the proper return stream of the raid. That was particularly difficult for individuals burdened with a load. This time, there were no fights between *F. sanguinea* and *L. fuliginosus*. Earlier, in a similar situation, in spite of all their aggressiveness and physical strength, *F. sanguinea* was virtually helpless when confronted with the determination of *L. fuliginosus* and with their remarkable chemical weapon (Czechowski 1999).

DISCUSSION

Wood ants and *Formica sanguinea* are highly competitive species. As Punttila et al. (1996) have shown basing on the topical state of ant communities, competition between them indirectly affect populations of some *F. sanguinea* slave species. The findings presented in this paper reveal (at least partly) the mechanism of this phenomenon. Wood ant colonies (as well as colonies of some other territorial ants), while protecting their own territories, do not enter raiding columns of *F. sanguinea* bound for slave species nests situated within their foraging areas. Of course, anything that keeps the slavemakers away from their potential victims is positive to them. On the other hand, however, it is a fact that subordinate species that live in a dominant's territory are subject to certain restrictions

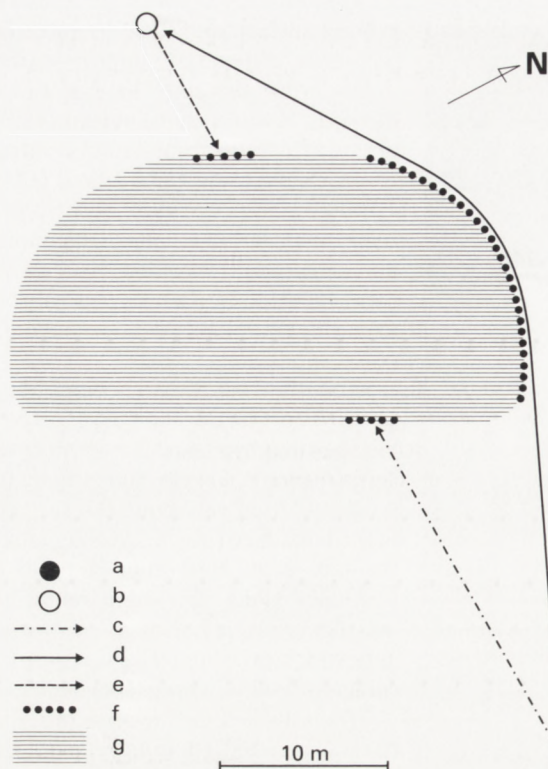


Figure 3. Course of the *F. sanguinea* raid in relation to the territory of *L. fuliginosus* (a – *F. sanguinea* nest, b – *F. cinerea* nest complex, c – intentional raid direction, d – actual raid route, e – direction of home-coming attempts of some *F. sanguinea* individuals, f – cordon of *L. fuliginosus* workers, g – *L. fuliginosus* territory; see also Fig. 4 in Czechowski 1999).

(see Introduction). It seems advisable to undertake comparative studies into the profit and loss account in *Serviformica* ants (especially *F. fusca*) within and outside territories of territorial species (particularly those of wood ants) in areas controlled by *F. sanguinea*.

F. sanguinea is a common species, and it frequently occurs in great numbers. This is coupled with a possibility of partial overlapping of the influence zones of nearby colonies. It is not uncommon that during one season the same nest of a slave species is plundered, in turn, by different *F. sanguinea* colonies, and during periods of particularly intensive activity of *F. sanguinea*, routes of raids from foreign colonies criss-cross or converge at the common goal (Czechowski, unpubl. data, see also Czechowski 1993, 1994). It is conceivable that *F. sanguinea*, being a facultative slave-maker – for which possession of slaves is not *conditio sine qua non* for the existence of its colonies but only a kind of luxury for them – may locally exterminate populations of slave species. Therefore, in areas where *F. sanguinea* occur, the role of colonies of territorial ants as structure-building elements of multi-species assemblages is very special. These species not only decide the spatial organization of ant assemblages but they also are a factor in retaining species diversity.

ACKNOWLEDGEMENTS

I thank referees, Riitta Savolainen, Jan Dobrzański, Graham Elmes and Francesco Le Moli, for reviewing and improving the manuscript. I am especially indebted to Riitta for her constructively critical comments and corrections. The field work was made during my stay at the Tvärminne Zoological Station, University of Helsinki.

REFERENCES

- Czechowski, W. 1975. Wyprawy rabunkowe mrówki *Polyergus rufescens* Latr. (Hymenoptera: Formicidae). *Przegląd Zoologiczny*, 19: 449–463.
- Czechowski, W. 1977. Recruitment signals and raids in slave-maker ants. *Annales Zoologici*, 34: 1–26.
- Czechowski, W. 1993. Czy kolonie *Formica sanguinea* Latr. (Hymenoptera, Formicidae) przejmują identyfikator zapachowy od swoich niewolnic? *Przegląd Zoologiczny*, 37: 273–276.
- Czechowski, W. 1994. Impact of atypical slaves on intraspecific relations in *Formica sanguinea* Latr. (Hymenoptera, Formicidae). *Bulletin de l'Académie Polonaise des Sciences*, 2. Classe, 42: 345–350.
- Czechowski, W. 1999. *Lasius fuliginosus* (Latr.) on a sandy dune – its living conditions and interference during raids of *Formica sanguinea* Latr. (Hymenoptera, Formicidae). *Annales Zoologici*, 49: 117–123.
- Czechowski, W. and W. Rotkiewicz. 1997. Relations between *Formica sanguinea* Latr. and *Formica cinerea cinerea* Mayr (Hymenoptera, Formicidae) – an unusual form of dulosis. *Annales Zoologici*, 47: 469–478.
- Pisarski, B. 1973. Struktura społeczna *Formica (C.) exsecta* Nyl. (Hymenoptera: Formicidae) i jej wpływ na morfologię, ekologię i etologię gatunku. Warszawa, 134 pp.
- Pisarski, B. 1982. Territoires et territorialisme de *Formica (Coptoformica) exsecta* Nyl. *Memorabilia Zoologica*, 38: 163–203.
- Pisarski, B. and K. Vepsäläinen. 1989. Competitive hierarchy in ant communities (Hymenoptera, Formicidae). *Annales Zoologici*, 42: 321–329.
- Punttila, P., Y. Haila, T. Pajunen and H. Tukia. 1991. Colonisation of clearcut forests by ants in the southern Finnish taiga: a quantitative survey. *Oikos*, 61: 250–262.
- Punttila, P., Y. Haila and H. Tukia. 1996. Ant communities in taiga clearcuts: habitat effects and species interactions. *Ecography*, 19: 16–28.
- Savolainen, R. 1990. Colony success of the submissive ant *Formica fusca* within territories of the dominant *Formica polyctena*. *Ecological Entomology*, 15: 79–85.
- Savolainen, R. 1991. Interference by wood ant influences size selection and retrieval rate of prey by *Formica fusca*. *Behavioral Ecology and Sociobiology*, 28: 1–7.
- Savolainen, R. and K. Vepsäläinen. 1988. A competition hierarchy among boreal ants: impact on resource partitioning and community structure. *Oikos*, 51: 135–155.
- Savolainen, R. and K. Vepsäläinen. 1989. Niche differentiation of ant species within territories of the wood ant *Formica polyctena*. *Oikos*, 56: 3–16.
- Savolainen, R., K. Vepsäläinen and H. Wuorenrinne. 1989. Ant assemblages in the taiga biome: testing the role of territorial wood ants. *Oecologia*, 81: 481–486.
- Vepsäläinen, K. and B. Pisarski. 1982. Assembly of island ant communities. *Annales Zoologici Fennici*, 19: 327–335.