

# LASIUS FULIGINOSUS (LATR.) ON A SANDY DUNE – ITS LIVING CONDITIONS AND INTERFERENCE DURING RAIDS OF *FORMICA SANGUINEA* LATR. (HYMENOPTERA, FORMICIDAE)

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**Abstract.**— The paper gives a description of a *Lasius fuliginosus* Latr. colony on a sandy dune, the ants' way of life in this beyond-optimum habitat, and their attitude towards other ant species (*Formica sanguinea* Latr., *F. cinerea* Mayr and *F. fusca* L.) revealed during raids of blood-red ants in the neighbourhood. The results are discussed in the context of hierarchical organization of ants species assemblages.



**Key words.**— Ants, *Lasius fuliginosus*, *Formica sanguinea*, *Formica cinerea*, *Formica fusca*, territoriality, interspecific hierarchy, competition, ecology.

## INTRODUCTION

*Lasius (Dendrolasius) fuliginosus* (Latr.) is an amphipalaearctic species; it occurs (except in high mountains) from Portugal to Japan and northern India and from southern Italy to southern Fennoscandia, where it reaches 62°N. On the basis of the ecological preferences of the species (Bernard 1968, Begdon 1954, Pisarski 1975, Kupyanskaya 1989 et al.) *L. fuliginosus* may be considered a mesohygrophilous and mesothermophilous oligotope of deciduous forests, that also enters mixed forests, parks and orchards.

As a typical dendrophile, *L. fuliginosus* builds nests in holes at the base of tree trunks and under the roots of old but living trees of different species. Its atypical nesting places, for instance in the sand of a sea dune in England have been reported by Donisthorpe (1915). A possibility of *L. fuliginosus* occurring on sandy dunes has also been mentioned by Collingwood (1979) in a monograph on the ants of Fennoscandia. The present paper may be considered an illustration of this general statement.

## TIME AND STUDY AREA

The observations were taken near the village of Tvärminne on the Hanko Peninsula, south Finland (59°50'E) in early July, 1998. The object was a *L. fuliginosus* colony chanced upon during studies into relations between *Formica sanguinea* Latr. and *F. cinerea* Mayr (see Czechowski 1997) carried out in a complex of sandy dunes which were becoming overgrown with pine wood. Earlier (in 1986), the structure and succession of ant assemblages had been studied there. At that time, 24 ant species were recorded, and with-

in these the presence of *L. fuliginosus* was reported on the basis of winged sexuals only (Gallé 1991).

An extensive description of the Tvärminne area has been given by Palmgren (1972). The vegetation of the local dunes is similar to that of other northern European habitats of this type (see Doing 1985). Faunistic peculiarities of the area have been recorded by Keynäs (1996).

## DESCRIPTION OF THE OBSERVATIONS

### Living conditions

The *L. fuliginosus* colony under discussion nested on the slope of a dune in and under an old pine stump (Fig. 1) situated in the centre of a semicircular patch of pine forest covering 350 m<sup>2</sup>. Nest entrances were directly at the base of the stump and also in sand about 50 cm downwards from the stump. In the patch, which had virtually no herb layer, there were over a dozen pines of different age and one branchy willow (*Salix cinerea*) (Fig. 2). The soil there was covered with a thick layer of needle litter, cones and dry twigs (Fig. 1); in places there was moss and lichen. In respect of the degree of advancement of dune vegetation succession this patch corresponded, after the 8-degree scale of Gallé (1991), to the 7th stage of succession.

The patch was distinctly separated from the neighbourhood. From above and on both sides it was surrounded by open sandy spaces, sparsely overgrown with *Carex arenaria* (3rd stage of succession). Its base was provided by a 4-metre-wide, hardly ever used sandy road that separated the patch from a belt of pine forest stretching along the foot of the dune (Figs 2 and 3) with a well-developed heather



Fig. 1. Stump with a *Lasius fuliginosus* nest on a dune in Tvärminne (photo W. Czechowski).



Fig. 2. Forest patch on the dune inhabited by *Lasius fuliginosus* (view from E) (photo W. Czechowski).



Fig. 3. Arena of the *Formica sanguinea*-*F. cinerea*-*F. fusca*-*Lasius fuliginosus* conflict: slope of the dune and the road separating the two parts of the *L. fuliginosus* territory; in the background and over the road is the forest patch, on the right is a belt of forest (view from S-W) (photo W. Czechowski).

(*Calluna vulgaris*) layer (the 8th and last stage of succession, after Gallé).

The territory of the *L. fuliginosus* colony comprised the forest patch on the dune slope (here the borderline of the foraging area was identical with a distinctly marked margin of the litter-covered area) and part of an about 250 m<sup>2</sup> forest belt on the other side of the road. So, the entire territory covered about 600 m<sup>2</sup>. Its two parts (actually separate foraging areas) were joined by an ant trail crossing the road at a right angle. The nest was situated merely 9 m south-east of the side of the road yet the trail from the nest to the crossing point led a sophisticated route of about 30 m. This roundabout way was clearly meant to shorten the unshaded part of the trail to the utmost. The ants had achieved that by going south from the forest patch towards two roadside aspens. In order to reach the shade of the trees they went along sand partly shaded by a granite boulder and then, after crossing the road (in the forest), they immediately turned north-eastwards (Fig. 4). Within the forest patch the ant trail led in a tunnel under litter.

The road was a stumbling block of the route. When most of its width was insolated, the ants abandoned the trail and gathered in the shade on both sides of the road. At the beginning of July, such everyday breaks in traffic lasted more or less 1.5 hour, from about 13.00 to 14.30. After a break, communication between the two parts of the territory was gradually restored and started the moment the insolated distance to negotiate had shrunk to about 0.5 m.

This particular trail was the longest and the most used one. It was nearly 40 m long, with about 15 m running along sheer sand. After crossing the road the ants marched in close order for about 3 m and then dispersed in the forest. There were two other, much shorter and less frequented trails from the nest. Both were entirely contained within the forest patch with the nest, and a greater part of either was hidden under litter. One of them led north-eastwards and after 10 m from the nest melted into the foraging area. The other, 8 m of which were on the ground, led north-westwards to (and up) the trunk of a 10-year-old pine growing at the end of the forest patch, at the highest point of the dune slope (Fig. 4).

This tree was the only one in the entire territory of *L. fuliginosus* that was visited by foragers in an organized way in order to milk aphids. Almost all ants returning to their nest along this trail had gasters filled with honeydew. Other trees were visited at most by single workers; relatively many individuals were observed attending aphids on the only willow in the forest patch. They were also seen together with other ants (*Myrmica* spp., *Leptothorax* spp.), all licking honeydew off leaves of several-year-old aspens growing on the edge of the forest on the other side of the road. Among workers returning to the nest via both trails which disappeared in litter the proportion of individuals with distinctly expanded gasters never exceeded 10%. However, most ants carried bits of solid food, mainly small invertebrates. It is noteworthy that the transported prey included fairly numerous big (for *L. fuliginosus*) and hard insects, such as curculionids and elaterids.

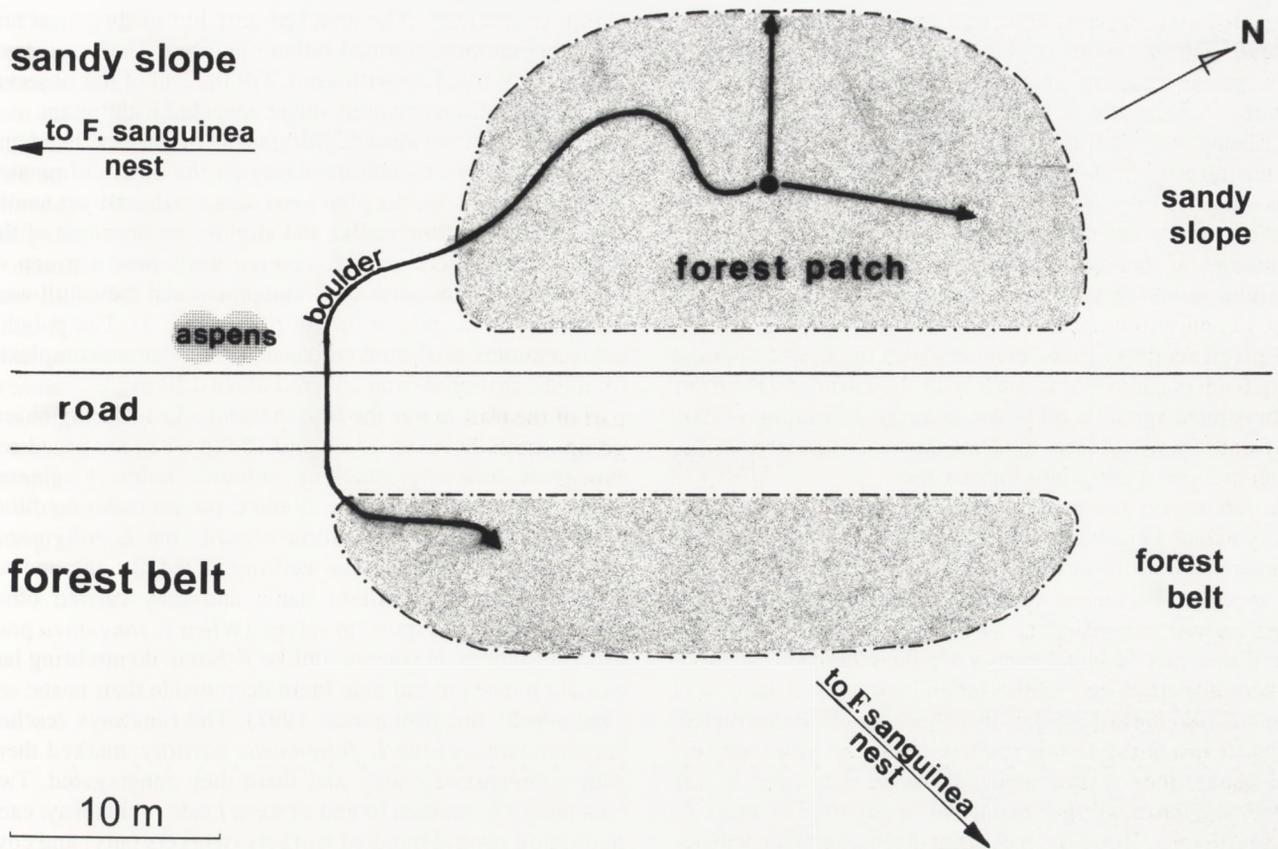


Fig. 4. Situation of the two-part territory of the *L. fuliginosus* colony and the course of its trails.

### Relations with other ants

In the territory of *L. fuliginosus* there were found nests of *Myrmica sulcinodis* Nyl. and *M. hellenica* For. [neither species was recorded from the Tvärminne dune by Gallé (1991)], *Leptothorax tuberum* (Fabr.), *L. acervorum* (Fabr.), *L. muscorum* (Nyl.), *Lasius alienus* (Foerst.), and *Formica fusca* L. Around the territory, in more or less open sandy areas, nested *Formica sanguinea* Latr., *F. cinerea* Mayr and other species.

No direct contests between *L. fuliginosus* and *Myrmica* and *Leptothorax* ants were recorded although in certain situations the latter caused some excitement in the former. In one case, a strangely increased density of *L. fuliginosus* workers was noticed at the northern end of the forest patch. It turned out that the ants were interested in plesiobiotic nests of *Myrmica hellenica* and *Leptothorax tuberum* hidden under litter. However, no encounters or brood robbery were recorded. In another case, *L. fuliginosus* ants became interested (but had not interfered directly) in a conflict between *Leptothorax acervorum* and *L. muscorum* that was taking place in litter. [This may have been a raid of *Harpagoxenus sublaevis* (Nyl.) and its *L. acervorum* slaves against a *L. muscorum* colony].

Normally, there were no conflicts between *L. fuliginosus* ants and single *Formica sanguinea* workers venturing into

their territory. However, an aggressive attitude of *L. fuliginosus* towards its neighbours was provoked by *F. sanguinea* raids on nearby numerous colonies of *Formica cinerea* and on less numerous colonies of *F. fusca*. The blood-red ants began their raiding activity in the area under discussion on 4 July. Conflicts between *F. sanguinea* and *F. cinerea* are always very dramatic and their results – unlike those during raids against *F. fusca* – cannot be foreseen (see Czechowski and Rotkiewicz 1997). The course of such conflicts observed on the Tvärminne dunes will be described in another paper.

On 6 July, active became a colony of *F. sanguinea* nesting under a boulder projecting from sand, over 40 m southwest of the territory of *L. fuliginosus*. The blood-red ants' three-day attacks were directed at polydomous complexes of *F. cinerea* on the slope and at the foot of the dune stretching between a *F. sanguinea* nest and the forest patch with *L. fuliginosus*. The conflict started at about 15.00 with a violent raid of blood-red ants simultaneously against several complexes of *F. cinerea* nests, among others on their linear paths in the ruts of the road which, 20–25 m away, were crossed by the trail of *L. fuliginosus*.

On the following day, between 13.00 and 14.00, the raid was continued along the old trail (aslant the dune and then along the road; Fig. 3), but this time it went farther on. *F.*

*sanguinea* attacked nest after nest of *F. cinerea* and one of *F. fusca* – all in the ruts of the road. A combat in which the three species were involved, was fought barely 3 m from the trail of *L. fuliginosus*, at 15.00. *F. cinerea* and *F. fusca* workers, fleeing side by side from *F. sanguinea*, headed towards the territory of *L. fuliginosus* and towards its trail. Soon, long (about 3 m) and narrow tongue-shaped streams of *L. fuliginosus* ants began to advance from the trail towards the boundaries of the territory (Fig. 5). The streams formed at different points of the trail, depending on the alien ants' place of concentration, but they withdrew when the "threat" to a given section of the boundary was over. The moment the defenders came into contact with the intruders, the front of the stream spread out (to left and right) forming a flexible front, from a dozen to some score centimetres wide, which prevented entry into the territory.

*L. fuliginosus* resorted to entirely passive defense. They clearly avoided encounters and simply blocked the way. The strangers' attitude towards *L. fuliginosus* varied depending on the species. *F. cinerea* workers, although panic-stricken, never crossed the boundary of the *L. fuliginosus* territory, even if they met no living barrier. On the other hand, *F. fusca* workers dispersed and single individuals picked their way among *L. fuliginosus* and thus managed, almost unobstructed, to get far inside the territory where (together with their rescued pupae) they waited until the danger was over. It was only *F. sanguinea* workers that occasionally tried to attack *L. fuliginosus* ants. However, they were discouraged immediately after the first contact and they vigorously rubbed their mandibles against sand for some minutes; their behaviour must have been due to the effect of dendrolasine, the specific defensive chemical weapon of *L. fuliginosus* (Pavan 1959).

On that day, only once did the excited *L. fuliginosus* ants manifest a really aggressive attitude, namely when they attacked an unoffending incipient colony of *Lasius alienus*

within its territory. The attacked ants hid in their nest and the only entrance, stormed rather clumsily by *L. fuliginosus*, was quickly filled up with sand. Till the end of the observations, the *L. alienus* colony never revealed itself again.

The conflict between *L. fuliginosus* on the one hand and *F. sanguinea* and its dulotic slaves on the other culminated on 8 July. At 14.30, the blood-red ants conducted yet another raid, but this time across and slightly up the slope of the dune. Their targets were *F. cinerea* nests near a group of boulders between a nest of *F. sanguinea* and the south-west margin of the *L. fuliginosus* territory (Fig. 3). The polydomous complex of *F. cinerea* consisted of four subcomplexes (A, B, C, D; Fig. 6) and covered about 120 m<sup>2</sup>.

Subcomplex A was the first to be attacked. During observations made between 15.30 and 16.00, when the blood-red ants were furiously attacking entrance holes, *F. cinerea* workers from Subcomplexes B and C (as yet under no direct threat) began mass evacuation towards the *L. fuliginosus* territory. The operation was well-organized, the ants moved in both directions without panic and they carried other workers (adult transport) to safety. (When *F. sanguinea* pose a threat to them, *F. cinerea*, unlike *F. fusca*, do not bring larvae and pupae out but hide them deep inside their nests; see Czechowski and Rotkiewicz 1997). The runaways reached the boundaries of the *L. fuliginosus* territory, marked there with a rampart of cones, and there they congregated. Two bivouacs of *F. cinerea* (b and c) were made in this way, each containing several hundred workers (workers only) and covering an area of not more than 0.25 m<sup>2</sup>. The ants there began barricading themselves in among the cones and for this purpose collected bits of litter from the neighbourhood. Soon (about 16.00), however, the ants from Bivouac c returned to their nests (adult transport again) and instantly went about making it deeper(!). This must have been the case because they were hastily carrying sand out of the nest entrances.



Fig. 5. Fragment of a tongue-shaped column moving from the *Lasius fuliginosus* trail towards the arena of the multispecies *Formica sanguinea*-*F. cinerea*-*F. fusca* conflict (photo W. Czechowski).

The observations were resumed after a two-hour interval (i.e. at 18.00) and then the situation was as follows: Subcomplexes A, B and C of *F. cinerea* had superficially been taken over by *F. sanguinea*; the blood-red ants – as is usual in such cases (Czechowski and Rotkiewicz 1997) – tried to uncover nest entrances closed on the inside by the defenders. *L. fuliginosus* ants, on the other hand, put guards along the part of their territory bordering on the complex of *F. cinerea*. While doing this, great numbers of them left their forest patch, entered open space and searched an 8-metre-long and 1–1.5-metre-wide stretch of sand. Moreover, when need required, they sent flexible tongue-shaped streams which searched the area within a distance of 2–3 m. *F. cinerea* workers from Bivouac b, forced by *L. fuliginosus* to retreat, were finishing their removal (adult transport) to Complex D which had been spared by *F. sanguinea*.

Within a quarter of an hour (around 18.15), the blood-red ants gradually, and voluntarily, left Subcomplex B. While

these were withdrawing, *F. cinerea* workers, which had dispersed over the neighbourhood, began to gather within this subcomplex; soon, adult transport to Subcomplex D was undertaken (nest entrances in their subcomplex remained closed). Simultaneously, a huge stream of *F. fuliginosus* advancing from the area of former Bivouac c of *F. cinerea* poured into Subcomplex C which was still occupied by *F. sanguinea*. The *F. fuliginosus* workers, moving in a dense column from entrance to entrance of *F. cinerea*, drove the blood-red ants away from the holes. The latter, after short attempts at fighting, fled in panic. *F. fuliginosus* were hardly interested in the freed *F. cinerea* nest entrances; with one exception, though, and in that case they vigorously and for some minutes tried to deepen an entrance barricaded from within. Neither did they pay much attention to *F. cinerea* ants returning to their territory as *F. sanguinea* were withdrawing from it.

The whole episode lasted about fifteen minutes. During that time, *L. fuliginosus* collectively killed two blood-red

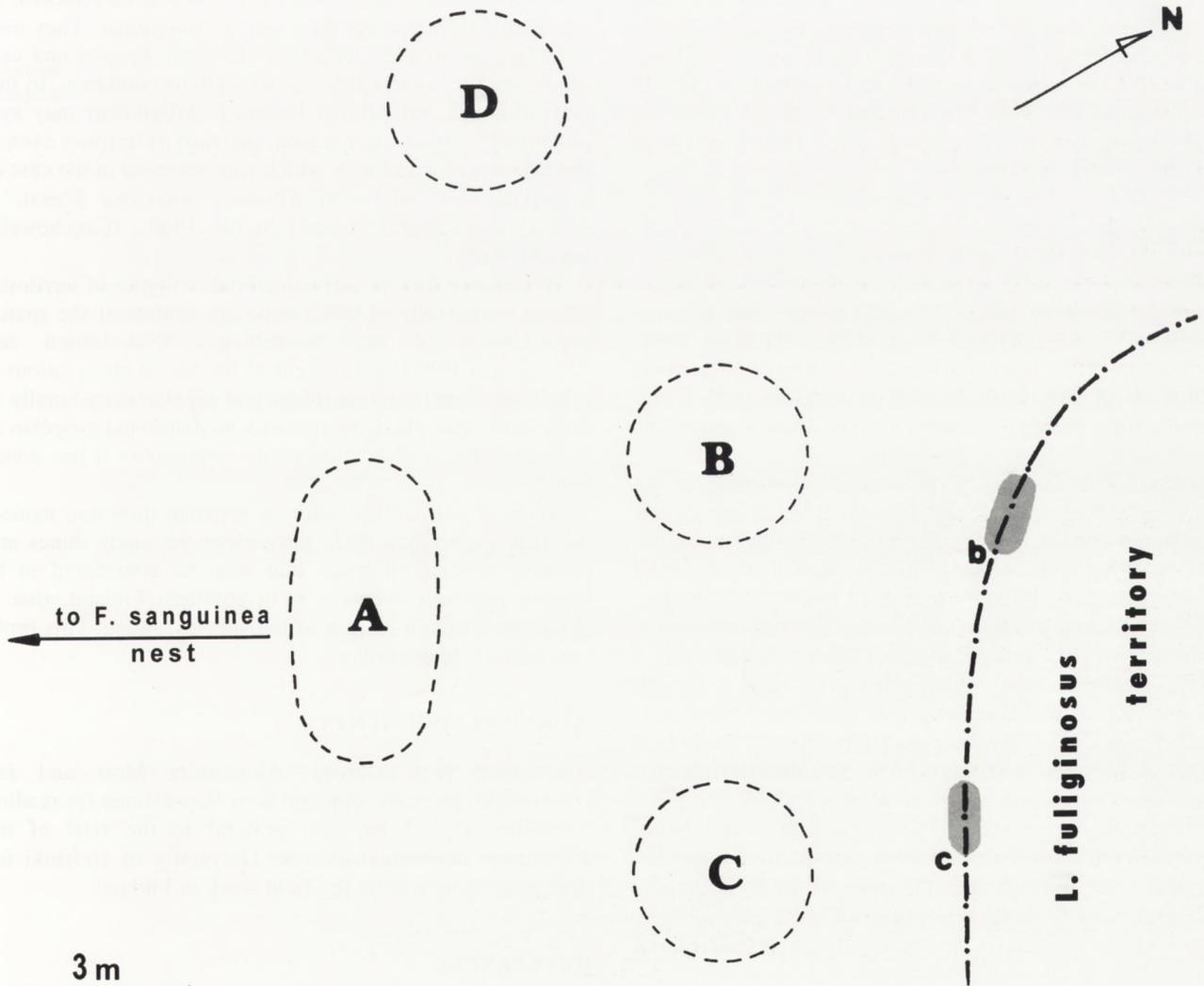


Fig. 6. Diagram of the *Formica cinerea* nest complex attacked by *F. sanguinea* – spot of *Lasius fuliginosus* interference in the conflict (A, B, C and D – *F. cinerea* subcomplexes, b and c – *F. cinerea* bivouacs).

ants that had not managed to escape, and here and there they contemplated half-dead or dead *F. cinerea* individuals which probably were casualties of the preliminary stage of the conflict with *F. sanguinea*. At a spot within Subcomplex C not reached by the stream of *L. fuliginosus* (5 m from the boundary of the latter's territory) there was a heap of dead specimens of all three species: 6 *F.s.*, 8 *F.c.* and 8 *L.f.* This was evidence that the already-described "liberation offensive" of *L. fuliginosus* had not been the first operation of these ants within their neighbour's territory on that day.

At 18.40, *L. fuliginosus* attacked once again and this time finally ousted the blood-red ants from Subcomplex C of *F. cinerea*. A little later, they also withdrew from Subcomplex A.

On the following day (9 July), there became active a colony of *F. sanguinea* nesting in the forest on the other side of the road. About noon, while marching along the edge of that part of the territory of *L. fuliginosus*, it attacked a *F. fusca* nest in the rut of the road. *F. fuliginosus* workers formed a dense cordon along the forest patch but this time, too, fleeing *F. fusca* with pupae passed through it unobstructed and took refuge in the territory of their neighbour. That was the last observation made in Tvärminne in 1998. In the light of earlier results it is justified to assume that if the blood-red ants had tried to chase *F. fusca*, they would have found the cordon impenetrable.

## DISCUSSION

Aggressiveness of *Lasius fuliginosus* towards *Formica* species (*F. pratensis* Retz., *F. rufa* L.) was already commented on a long time ago (Forel 1874, Wasmann 1899, Donisthorpe 1915). Intolerance manifested by *L. fuliginosus* towards wood ants was stressed by Begdon (1954) who warned against attempts at artificial introduction of the latter into areas belonging to the former.

According to the theory of hierarchic structure of ant assemblages (Vepsäläinen and Pisarski 1982, Pisarski and Vepsäläinen 1989) *L. fuliginosus*, as an aggressive and territorial species (Dobrzańska 1966, Savolainen et al. 1989) represents the 3rd and highest level of interspecific hierarchy. *Formica sanguinea* and *F. cinerea* belong to the same hierarchic category and the former must be described as a specific territorial form which, during its raiding period, does not respect the boundaries of other ants' territories. *Formica fusca* (like *Myrmica* and *Leptothorax* ants) is a non-aggressive, non-territorial species (a submissive form); it represents the 1st and lowest level of hierarchy.

The mutual attitudes of the ants involved in the above-mentioned conflict revealed what position particular species occupied in the interspecific hierarchy of the local assemblage, especially in its uppermost part. The top position was occupied by *L. fuliginosus* predominating over the others even outside its territory. The second belonged to *F. sanguinea*; relations between these two dominating species were highly aggressive. The third position, and the last within the highest hierarchic level (i.e. in territorials), must

go to *F. cinerea*. Firstly, it was the victim of *F. sanguinea* raids and secondly, it definitely manifested subordination to *L. fuliginosus*; for *F. cinerea* ants the boundary of the latter's territory was impassable even in a situation of, so to say, the "higher necessity".

It was different with *F. fusca*. As a submissive and so-called opportunistic form it may not only enter the foraging areas of territorial species but it even may nest near their colonies. *F. fusca* are extremely able-bodied ants that find it easy to pick their way even among dense masses of wood ants, let alone among *L. fuliginosus*.

*L. fuliginosus* made a minor attack upon a small nest of *L. alienus*, an aggressive but probably non-territorial species belonging to the middle, i.e. second hierarchic group. That attack may have been the so-called redirected aggression, when aggression to the real opponent which as yet must be curbed, is replaced at another object.

The way in which *L. fuliginosus* fights may be described as "passive pressure". These slow and weak ants simply push towards the enemy and let themselves be attacked, as was the case in the conflict with *F. sanguinea*. They owe their success to their unfailing chemical weapon and certainly neither to their physical strength nor numbers. In this way, although not without losses, *L. fuliginosus* may systematically, season after season, increase its territory even at the expense of wood ants, which was observed in the case of a polydomous colony of *Formica polyctena* Foerst. at Celestynów (central Poland) in the 1960s. (Czechowski, unpubl. data).

It is known that, in a given habitat, colonies of territorial species (especially of wood ants) are centres of the spatial organization of ant assemblages (Savolainen and Vepsäläinen 1988). In the light of the above observations it is possible to anthropomorphize and say that occasionally *L. fuliginosus* also plays the role of a mediator and guardian of the status quo in the multispecies community it has dominated.

There is yet another, entirely separate question, namely the very occurrence of *L. fuliginosus* on sandy dunes and possibly in other habitats that may be considered to be beyond-optimum ones for it in southern Finland, that is along the northern margin of the species' range. This problem wants further studies.

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