

*FORMICA RUF*A L. PROTECTS INDIRECTLY *F. FUSCA* L. AGAINST RAIDS OF *F. SANGUINEA* LATR. (HYMENOPTERA: FORMICIDAE)

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Abstract.— By protecting their territory against all territorial ants, *Formica rufa* L. indirectly protected *F. fusca* L., nesting within their territory, against *F. sanguinea* Latr. raids. The permanent costs to *F. fusca* caused by highly aggressive *F. rufa* within their territories were outweighed by the benefits obtained by *F. rufa*'s protection against periodic raids of *F. sanguinea*. We interpret our findings in the light of the hierarchy competitive framework as follows.



Key words.— Ants, *Formica fusca*, *F. rufa*, *F. sanguinea*, territoriality, competition hierarchy, interspecific competition, slavery.

INTRODUCTION

Multi-species ant assemblages in many northern boreal and temperate ecosystems have a hierarchic structure. They are dominated by territorial species that defend their foraging areas (Pisarski 1973, 1982, Vepsäläinen and Pisarski 1982, Savolainen and Vepsäläinen 1988). Nests of territorial ants form centres of spatial organization of local communities (Savolainen and Vepsäläinen 1988, 1989, Savolainen *et al.* 1989). Subordinate (non-territorial) ant species may live in a dominant's territory, but their abundance is lower (Punttila *et al.* 1991), foraging activity reduced and reproductive output lower, and they may nest only at a certain distance from the dominant's colony – the farther away the more competitive with the dominant the species is (Pisarski and Vepsäläinen 1989). Relations between the top dominant wood ant *Formica polyctena* Först. and *F. fusca* L. as a subordinate, submissive species that avoids all extra-nidal fights, reveal the heart of the matter perfectly (see Savolainen 1990, 1991): *ceteris paribus*, the success of subordinate ants is higher outside than inside territories of top dominant species.

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 the blood-red ant, *F. sanguinea* Latr., and wood ants of the *F. rufa* group indirectly affects the distribution and abundance of the potential slave species

(including *F. fusca*) of blood-red ants. Recently, direct interference of territorial ants, *Lasius fuliginosus* (Latr.) and *Formica rufa* L., in the course of *F. sanguinea* raids on nests of *F. fusca* have been described; this interference was beneficial to colonies of the latter species (Czechowski 1999, 2000). During their raiding period, *F. sanguinea* ants respect no boundaries of other species' territories, including those of wood ants. Wood ants defend their territories and at the same time protect, quite effectively, within-territory *F. fusca* colonies against *F. sanguinea*.

This prompts the question of *F. fusca*'s balance of profits and losses connected with nesting in territories of wood ants (or of any territorial ant) in areas situated within reach of *F. sanguinea*. Earlier observations (Czechowski 2000) suggest the hypothesis that in areas under the threat of blood-red ant raids, *F. fusca* are more abundant within than outside territories of wood ants, in spite of all the negative pressure exerted by the colony of the territorial species on populations of the subordinate species, including those of *F. fusca* itself (Savolainen 1990, 1991, Punttila *et al.* 1991). The present study is aimed at testing this hypothesis.

STUDY AREA, METHODS AND MATERIAL

The main investigations were carried out in July 2000 in a complex of sand dunes growing pine forest, near the village of Tvärminne on the Hanko Peninsula, S Finland

(Fig. 1). That had been the site of the above-mentioned observations on interference of territorial ants during *F. sanguinea* raids (Czechowski 1999, 2000).

The present study records ants at baits set in places occupied by *F. rufa* and *F. fusca* but lying within the range of *F. sanguinea* raids. Baits were put on the ground, every 2 m in a line so that one part of the transect was within and the other was outside the territory of *F. rufa*, or of any other territorial ant species (Fig. 2). The bait closest to the wood ant nest was 5–7 m from the mound. The entire line of baits ran within a belt of homogeneous habitat. At first (for *F. rufa* Colony I; see below) two kinds of bait were used in turn: carbohydrate baits (with fruit syrup) and protein ones (with fish paste). However, since *F. fusca* were relatively little interested in the fish paste, only syrup baits were used in latter experiments (with Colony II and with the Control one).

The Control experiment (in a habitat free of blood-red ants) was conducted in August 2000 in Puszcza Białowieska, NE Poland. The rationale for choosing the control from a different geographical region and habitat than the focal areas was to make sure that the control included the *F. rufa* territory and an immediately neighbouring area without *F. sanguinea* or any other territorial species.

In each case, within three days, nine series of readings were carried out at different times of the day, and the bait was replenished when necessary. On the basis of the presence (or absence) of *F. rufa* workers at or near a given bait we determined what part of the transect was within the boundaries of the territory of a wood ant colony. The number of *F. fusca* workers, and of other subordinate species, was recorded for each bait. *F. fusca* are so-called opportunistic ants, submissive to foragers of species which are higher in the interspecific competition hierarchy. Therefore, additionally to *F. fusca* individuals present at a given bait, also those interested in the source of food and moving around within a 10-cm radius from it were recorded. This proved right particularly in the control experiment in Puszcza Białowieska where all syrup baits along the transect were occupied by wasps, *Vespula vulgaris* (L.), and therefore ants had much more difficult to access them.

In Finland, two transects with bait (I and II) were established, each in close vicinity to a different colony of *F. rufa* (I and II). Colony I nested on the NW edge of a pine forest below a dune (mound diameter 150 cm, height 50 cm). Its territory covered part of the forest and a fragment of treeless ecotone belt (4–6 m wide; 10 m at the *F. rufa* nest) where the sand was covered with a layer of lichens and low moss. Under the moss, there were numerous nests of *F. fusca*. These nests were a target of annual raids of *F. sanguinea* colonies nesting on the upper edge of the dune (Fig. 1). There were four colonies of blood-red ants, and three of them (I, III and IV; Fig. 2) used to attack *F. fusca* colonies in the ecotone belt; this was observed each year from 1996 to 2000. These conflicts (in which Colony I of *F. rufa* participated) served as

part of material for a description of wood ant interference in the course of *F. sanguinea* raids (see Czechowski 2000). Colony II of *F. sanguinea*, located in front of the *F. rufa* mound (Fig. 2), was never seen to raid *F. fusca* nests in the ecotone.

The 100-m transect had 51 baits, and ran along the middle of the ecotone belt, traversing the territory of *F. rufa*; 30 baits (15 at each end) were outside and 21 within the territory of wood ants (Fig. 2). The transect, although in the zone of *F. sanguinea* raids, was beyond the reach of foragers of this species; no blood-red ant was recorded at any of the baits.

Colony II of *F. rufa* nested on the SE edge of the same forest and the dimensions of its mound were as for Colony I of *F. rufa* above. Its territory comprised part of the forest and a fragment of dry meadow populated, among others, by *F. fusca*. In one corner of the meadow, about 30 m from the *F. rufa* mound, nested a huge *F. sanguinea* colony with enslaved workers of *F. fusca* (Fig. 3). The 48-m long transect with 25 baits run across the meadow towards the corner with the nest of blood-red ants. The first 13 baits were within and the last 12 were outside the territory of wood ants. The latter baits, except the one nearest to the territory boundary, were exploited by *F. sanguinea* foragers.

The 100-m Control transect in Poland, with 51 baits, ran along an ecotone between the S edge of an oak forest and a vast forest meadow. The 3–8-m wide ecotone belt was covered with sparse gramineous vegetation and separated from the meadow by a dirt road (Fig. 4). The *F. rufa* mound on the edge of the forest was much smaller than the Finnish ones (diameter 50 cm, height 30 cm). The first 25 baits of this transect were within and the remaining 26 baits outside the territory of *F. rufa*, or of any other territorial ant.

Statistical tests are one-sided and made with Stata Statistical Software (StataCorp 2001), except log-linear modelling of $2 \times 2 \times 2$ tables (Systat 1989). For the control, and all other species than *F. fusca* along the transects I and II, the expected species-specific (or genus-specific) abundance or occurrence on the baits, was higher outside than within the *F. rufa* territory, given a difference exists. If *F. rufa* gives a protective shield to *F. fusca* within the raiding distance of *F. sanguinea*, then the expected difference is for higher abundance and occurrence on the baits within the wood ant territory.

RESULTS

Formica fusca

The abundance of *F. fusca* in the control transect, free of *F. sanguinea*, was higher beyond than within the *F. rufa* territory (Table 1; $t = 3.24$, $df = 49$, $P = 0.002$). Outside the territory, the recorded number of *F. fusca* workers was 1.6 times as high as within it, in spite of the relatively small size of the control *F. rufa* colony. In areas where the *F. fusca* population was under the threat of



Figure 1. Dune habitat at Tvärminne – the place of the experiment at Colony I of *F. rufa*; nest location (Fr) marked. On the right, between a pine forest and an open sand dune, the moss-covered ecotone belt is settled by *F. fusca*. Colonies of *F. sanguinea* nest on the upper edge of the dune on the left (photo W. Czechowski).



Figure 3. Dry meadow at Tvärminne – the place of the experiment at Colony II of *F. rufa*; nest location of *F. rufa* (Fr) and that of *F. sanguinea* (Fs) marked (photo W. Czechowski).



Figure 4. Habitat of the control experiment in the Białowieża Forest. The transect with baits run along a grassy ecotone belt between a road and an oak forest on the right; nest location of *F. rufa* (Fr) marked (photo W. Czechowski).

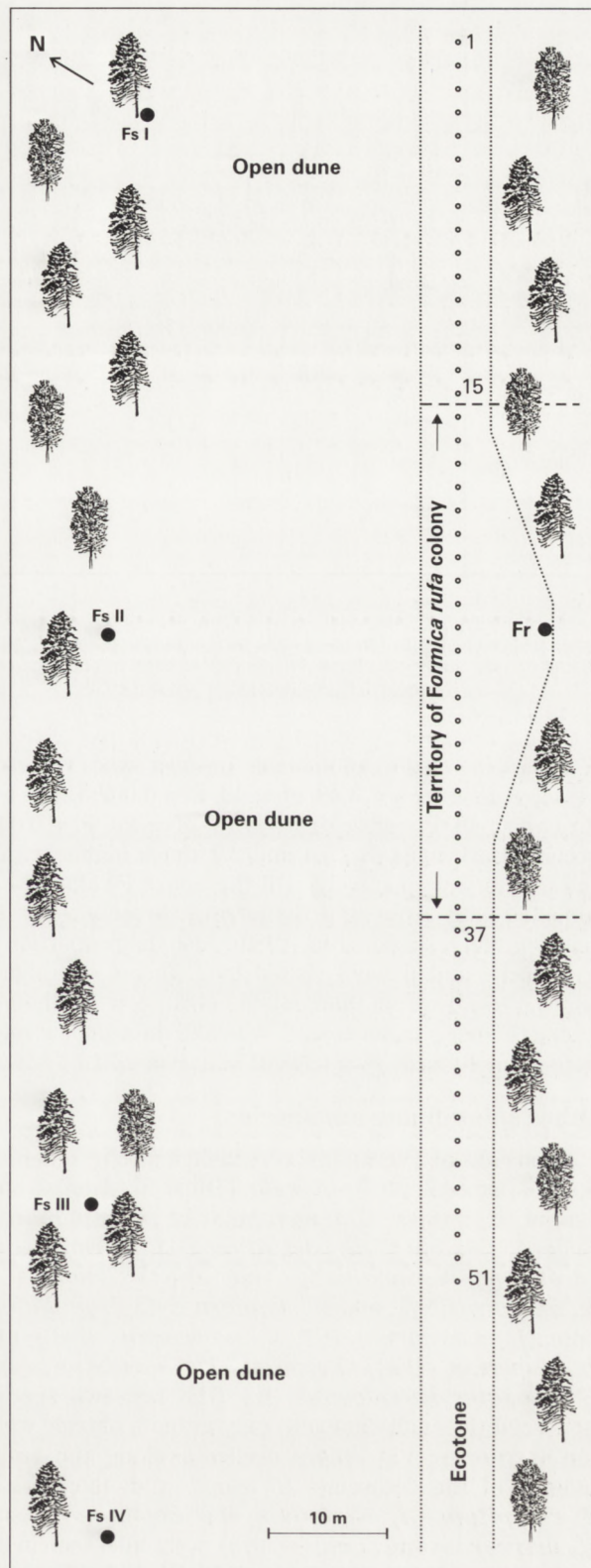


Figure 2. Location of the bait transect I near Colony I of *F. rufa* (Fr) against a background distribution of *F. sanguinea* nests (Fs) and an outline of the topography of the dune habitat (1...15...37...51 – numbers of baits).

Part of transect	Parameter	<i>F. fusca</i>	<i>L. niger</i>	<i>T. caespitum</i>	<i>M. ruginodis</i>	<i>Leptothorax</i> spp.
Within (25)	Mean	12.5	3.2	0.1	0.1	0.1
	SD	7.15	11.44	0.28	0.44	0.28
	Median	12	0	0	0	0
	Maximum	26	57	1	2	1
	I	100	28	8	8	8
Outside (26)	Mean	19.8	31.1	+	+	+
	SD	8.90	51.93	0.20	0.20	0.20
	Median	19	12	0	0	0
	Maximum	37	200	1	1	1
	I	100	85	4	4	4

Table 1. Summary of nine counts within three days of ant workers on syrup baits along Control transect (with no *F. sanguinea* around) within and outside the *F. rufa* territory (number of baits in parentheses); I – percentage of baits occupied, + – mean < 0.05.

F. sanguinea, the abundance pattern was reversed (Table 2; I/syrup: $t = 3.48$, $df = 49$, $P = 0.002$, I/fish: $t = 3.24$, $df = 49$, $P = .002$, II: $t = 5.15$, $df = 23$, $P = 0.000$; recorded averages 6.1, 5.4 and 3.7 times higher within the territory, respectively). All the above P-values were adjusted with sequential Bonferroni correction for the four parallel tests (see Rice 1989). Also the proportion of Transect I and II baits visited by *F. fusca* was higher (82%, $n = 55$) within than outside (43%, $n = 72$) the territory (Fisher's exact test, $P = 0.000$; data pooled after heterogeneity test, $\chi^2 = 0.59$, $df = 2$, $P = 0.74$).

Other subordinate ant species

The baits at Tvärminne were visited also by other ant species subordinate to *F. rufa* (Table 2): *Lasius* spp. [mainly *L. niger* (L.) and also *L. psammophilus* Seifert], *Tetramorium caespitum* (L.), *Myrmica* spp. [mainly *M. ruginodis* Nyl. and also *M. rubra* (L.), *M. lobicornis* Nyl., and *M. rugulosa* Nyl.], *Leptothorax* spp. [*L. acervorum* (F.), *L. muscorum* (Nyl.) and *L. tuberum* (F.)], *Formica rufibarbis* F., and *Camponotus herculeanus* (L.). The last two species appeared (in small numbers) only at baits outside wood ant territories; the others occurred along the entire lengths of the transects. *L. niger*, and sporadically, *T. caespitum*, *M. ruginodis* and *Leptothorax* spp. (*L. acervorum* and *L. muscorum*), were also seen in the entire control transect in Puszcza Białowieska (Table 1).

The average abundances and proportions of baits occupied by the other subordinate species outside vs within the *F. rufa* territory varied much (maximally about ten-fold average recorded for *L. niger* in the Control area).

Transect	Part of transect	Parameter	<i>F. fusca</i>	<i>Lasius</i> spp.	<i>T. caespitum</i>	<i>Myrmica</i> spp.	<i>Leptothorax</i> spp.	<i>F. rufibarbis</i>	<i>C. herculeanus</i>	
I (syrup)	Within (21)	Mean	4.9	11.0	2.2	24.0	4.7	0	—	
		SD	5.28	21.89	7.29	24.33	5.34			
		Median	3	0	0	17	3			
		Maximum	18	72	33	72	19			
		I	81	48	24	86	76	0	—	
	Outside (30)	Mean	0.8	28.8	12.6	52.2	6.3	0.2	—	
		SD	1.88	36.85	28.78	67.78	6.06	0.82		
		Median	0	8	0	9	4.5	0		
		Maximum	8	125	124	220	24	4		
		I	30	77	37	90	87	10	—	
	I (fish)	Within (21)	Mean	2.7	9.6	4.7	0.3	0.1	0	0
			SD	3.05	25.98	13.31	0.90	0.36		
Median			1	0	0	0	0			
Maximum			10	115	59	4	1			
I			71	33	19	14	14	0	0	
Outside (30)		Mean	0.5	10.5	34.6	1.8	0.3	0.3	0.1	
		SD	0.73	15.17	78.59	3.80	0.80	0.84	0.40	
		Median	0	3.5	0	0.5	0	0	0	
		Maximum	3	48	265	20	3	4	2	
		I	40	70	33	50	20	17	7	
II	Within (13)	Mean	14.5	23.1	6.8	48.2	2.3	—	0	
		SD	6.62	52.18	126.53	25.10	3.71			
		Median	14	0	0	45	0			
		Maximum	25	183	30	105	11			
		I	100	38	38	100	38	—	0	
	Outside (12)	Mean	3.9	14.3	54.7	93.7	5.4	—	0.7	
		SD	3.50	36.27	75.38	49.53	5.84		0.98	
		Median	3.5	0	22	93.5	4.5		0	
		Maximum	11	128	239	183	15		2	
		I	83	42	58	92	58	—	33	

Table 2. Summary of nine counts within three days of ant workers along Transect I (syrup and fish baits) with closelyby *F. sanguinea* colonies (see Fig. 2) within and outside the *F. rufa* territory, and along Transect II (syrup baits) with a closelyby *F. sanguinea* colony; — not recorded along the transect (for other explanations, see Table 1)

The distribution of the other subordinates on the baits was often highly clumped (*cf.* averages, standard deviations and medians in Tables 1 and 2). Because testing separately all species in all areas for intra- and extraterritorial abundances or occurrences would ruin the statistical power of the tests, we used from Tables 1 and 2 only those species with at least 20% of baits outside the *F. rufa* territory occupied (thus leaving *L. niger* in Table 1 and dropping *F. rufibarbis* and *C. herculeanus* in Table 2). Now 12 of the recorded averages were higher and one lower outside the territory ($H_0 = 6.5$ higher, 6.5 lower with no territoriality effect): $\chi^2 = 7.69$, $df = 1$, $P = 0.003$; the same result holds when proportions on baits were used. When those cases were dropped from the analysis, where the higher/lower average ratio was <2 , all the remaining ten pairs of averages had higher values outside than within the territory ($\chi^2 = 6.23$, $df = 1$, $P = 0.006$).

F. fusca. All lower-level models rendered highly significant discrepancies with the tables ($P = 0.000$).

DISCUSSION

In view of the complexity of interspecific competition structures in ants, the abundance of foragers at baits is not a faultless measure of the size of the population in a given area. However, the hypothesis put forward in the Introduction was supported by our present findings: to *F. fusca*, living as a submissive species in the territory of wood ants, the advantages of the protection of its nests from PERIODIC raids of *F. sanguinea* outweigh the PERMANENT disadvantages of the close proximity of the dominant species. Punttila *et al.* (1996) reached a similar conclusion by pitfall trapping in taiga clearcuts in southern Finland: competition between the wood ants and *F. sanguinea* affected indirectly the distribution and abundance of both potential slave species present, *F. fusca* and *F. lemni*. Also, in their preliminary studies in Tvärminne, R. Savolainen and K. Vepsäläinen (unpublished) recorded in areas covered by *F. sanguinea* raids higher densities of *F. fusca* nests (and not just relative abundances of individuals) within territories of wood ants than outside them.

Territorial, local top dominants of ant assemblages seem to give the same protection to potential slave species of *F. sanguinea*, independently of the species of the dominant. *F. cinerea* may locally monopolize vast areas by filling suitable dune areas with its nests; this is true also in our study area, the Hanko Peninsula. However, smaller, isolated colonies are targets of *F. sanguinea* raids similarly as are colonies of *F. fusca* and other most frequently used slaves. In such a situation, *F. cinerea* was seen to get protection against *F. sanguinea* raids by the local, highly territorial top-dominant *Lasius fuliginosus* (Czechowski 1999).

Our result should not be interpreted as an adaptive tactic that would bias young *F. fusca* queens (or queens of other potential slave species) somehow towards territories of potential protectors. On the contrary, it seems that queens have a better chance to found a nest, or even to survive, outside territories intensively searched by wood ants. We suggest that for *F. fusca* fundatrices wood ants are a bigger threat than *F. sanguinea* whose workers normally forage in much lower densities and whose raids are limited in time and space.

Thus the spatial differentiation in the abundance of *F. fusca* must be due to the pressure exerted by *F. sanguinea* on the available, already existing colonies of the former species. On one hand, this pressure obviously results in weakening – or even extinguishing – periodically raided colonies of *F. fusca*. On the other hand, it is possible that a part of the *F. fusca* population within the wood ant territory is reinforced by emigrants (workers or probably even queens) from colonies situated outside. During *F. sanguinea* raids, *F. fusca* workers were seen fleeing, with their pupae, from the raid zone and entering

	Species/part of transect		Abundance			
			Absent	Present		
(a)	<i>F.fusca</i>	Within	0 (0)	25	Best model for both (a) and (b): Species * Abundance * Within/Outside (=saturated model, exact fit with the table)	
		Outside	0 (0)	26		
	<i>L.niger</i>	Within	18 (72)	7		
		Outside	4 (15)	22		
(b)	Species/part of transect		Abundance			All other (lower-level) models: P=0.000 (i.e., statistically highly unsatisfying)
			<10	>9		
	<i>F.fusca</i>	Within	10 (40)	15		
		Outside	4 (15)	22		
	<i>L.niger</i>	Within	23 (92)	2		
		Outside	12 (46)	14		

Table 3. Multiway (Species * Within/Outside * Abundance) tables of abundances of *F. fusca* and *L. niger* on baits within and outside Control territory of *F. rufa* (with no *F. sanguinea* around); (a) – cutpoint for abundance: absent *vs* present, (b) – cutpoint for abundance: <10 *vs* >9 . Additionally to absolute frequencies, row percentages are given in parentheses for each cell of lower abundance

The proportion of baits occupied by *Lasius* spp. was statistically significantly higher outside (72%, $n = 98$) than within (36%, $n = 80$) *F. rufa* territories (Fisher's exact test, $P = 0.000$; data pooled after heterogeneity test, $\chi^2 = 4.51$, $df = 3$, $P = 0.21$). The difference between within *vs* outside abundances on baits of *L. niger* in the Control area, was also stronger than for *F. fusca*. Our $2 * 2 * 2$ tables (one with abundance cutpoint absent *vs* present, and another with <10 *vs* >9 ; Table 3) were both statistically satisfyingly fit by one model: Species * Within/Outside * Abundance. This saturated model has by definition a complete fit with the tables, and tells (together with Table 3) that the abundances of the species on the baits were higher outside than inside the territory, and that the difference was stronger for *L. niger* than for

unhindered the *F. rufa* territory across a (impenetrable to blood-red ants) boundary cordon of wood ants (Czechowski 2000). The same phenomenon was observed at the boundary of the territory of *Lasius fuliginosus* (Czechowski 1999). It is possible that some of these fugitives never return to their looted nests but settle in the area where they have found shelter – especially if they have a queen. Frequently, queens of potential slave species flee from nests attacked by *F. sanguinea* (Czechowski 2001 and unpublished observations).

Even though mature colonies of *F. sanguinea* are territorial, they are subordinate to moderately sized colonies of the *F. rufa* – group. Therefore, as comes to other species than potential slaves of *F. sanguinea*, their abundances are higher outside than inside territories of the *F. rufa*-group (Savolainen and Vepsäläinen 1988, 1989). This was also found in the present study, irrespective of the presence of *F. sanguinea*, for the assembly of subordinate species, using similar robust tests with similar result as Savolainen *et al.* (1989), Punttila *et al.* (1991), and Vepsäläinen *et al.* (2000).

However, subordinate ants classify to two, significantly different groups at two basic levels of the competition hierarchy: submissives at the bottom level, and encounter species between territorials and submissives (Vepsäläinen and Pisarski 1982). Although the foraging and nesting success, and nest densities, of submissive species tends to be lower within than outside territories of top dominants, they still nest within territories (Savolainen and Vepsäläinen 1988, 1989; Savolainen 1990, 1991). Because encounters defend both their nests and concentrated food sources, they easily run into strong physical conflicts with territorials. Owing to this, territorial species exert a much higher negative impact on encounters than on submissive species (Savolainen *et al.* 1989) – a result reached in the present study, too, while comparing *L. niger* and *F. fusca*. Strongest *F. rufa*-group colonies monopolize areas within a radius = 60 m from their mound, and keep practically all *L. niger* nests and foragers beyond the limits of the territory (Savolainen and Vepsäläinen 1989).

We conclude that the effect of local, territorial top-dominants is to decrease the foraging and nesting success of all subordinate species. This generalization does not go without species-specific exceptions, mostly explainable on the basis of morphological and behavioural differences between the subordinates and dominants (Savolainen and Vepsäläinen 1989). However, potential slave species used by *F. sanguinea* are a special case of species suffering from territoriality of top dominants: within the limits of raids by the blood-red ant, this suffering is turned to a cost of keeping the raiders out of reach – beyond the protective shield of strong territorials the losses are larger than the costs.

Our conclusion gets extra strength from three basic notions on the present study. First, *F. sanguinea* is not an effective slave-maker (many of its colonies lack slaves), and judging on the basis of much lower observed

slave proportions in the workforce of the blood-red ant in Finland than in areas closer to the center of its distribution, the raiding pressure on *F. fusca* is probably lower in our study area than in most other areas more south (see Czechowski 1996). Second, the protective *F. rufa* colonies were maximally of moderate size in reference to colonies of the northern boreal habitats. Moreover, in our study, the protection was given by single-mound colonies, whereas in the taiga and the eastern temperate regions the mean number of *F. rufa*-group mounds is rather 3–3.5 ha⁻¹ (Rosengren *et al.* 1979), and large (sets of) multinest colonies cover several tens of square kilometers (H. Wuorenrinne, unpublished), reaching locally mound densities of 180 ha⁻¹ (Marikovskiy 1962) and surviving half a millennium (Oinonen 1958).

Correction

A previous paper (Czechowski 1999) on interference of *Lasius fuliginosus* in the course of *F. sanguinea* raids on the Tvärminne dunes includes information, cited after Gallé (1991), that *L. alienus* (Först.) occurred there. In the meantime, however, Seifert (1992) revised the subgenus *Lasius* s.str. and split *L. alienus* into three species. Thus the species on the Tvärminne dunes was *L. psammophilus*, and not *L. alienus*.

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