

LASIUS PSAMMOPHILUS SEIFERT AND FORMICA CINEREA MAYR (HYMENOPTERA: FORMICIDAE) ON SAND DUNES: CONFLICTS AND COEXISTENCE

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Abstract. — *Lasius psammophilus* Seifert and *Formica cinerea* Mayr can both be found on sand dunes in high densities. Sometimes they even nest in each other's immediate neighbourhood, which implies the possibility of conflicts, and the existence of mechanisms for avoiding contest competition. In such case an appropriate method is the analysis of the distribution and behaviour of foraging individuals around their colonies in the absence and in the presence of baits. The results show that the higher foraging activity of *L. psammophilus* with lower temperature and higher humidity as compared to *F. cinerea*, as well as the lack of spatial interference assures a relatively peaceful coexistence even in the case of neighbouring colonies. While *L. psammophilus* is characterized by fortuitousness regarding the chances of discovering food sources, *F. cinerea* foragers search more thoroughly around their colonies. Conflicts can arise over large food sources, which conflicts are usually won by *F. cinerea*. However, the more efficient recruitment system of *L. psammophilus* (earlier start and higher intensity), allows this species dominate at clumped food patches when the climatic conditions are favourable. The possible ways of coexistence are discussed, as well as the species' positions in the competition hierarchy.



Key words. — ants, *Lasius psammophilus*, *Formica cinerea*, dynamics, competition, interactions, foraging strategies, interspecific hierarchy.

INTRODUCTION

Competition is an interaction among individuals, societies and populations in quest of the same values. In the case of species with similar requirements this may result in their ecological separation, in accordance with the principle of competitive exclusion (Hardin 1960); there may also develop peculiar adaptations that minimize the effects of competition (see Brown and Wilson 1956, Odum 1971, Krebs 1985). As the majority of ant species are omnivorous and a lot of them are eurytopes, their ecological niches and their habitat requirements frequently overlap to a greater or lesser extent. This may lead to severe interspecific competition, often of the contest type (Vepsäläinen 1980).

On the other hand, in a vast majority of habitats, ants form qualitatively stable multi-species assemblag-

es, which is evidence of some degree of equilibrium achieved through evolutionarily fixed adjustments of species. In ants, a peculiar system of hierarchic subordination of species is the essence of such adjustment, i.e. a system that regulates the rules of exploitation of shared resources and limits energy-consuming and devastating conflicts. The species are hierarchically arranged on the basis of social organization of their colonies (mainly colony size, forager density and recruitment efficiency) and the hierarchy consists of three main competition levels. These are (beginning with inferior competitors): submissive species (defending only their nests), encounter species (defending food sources in addition to defending their nest) and territorial species (defending their whole foraging areas; colonies of such species replace one another in space) (Vepsäläinen and Pisarski 1982, Savolainen and Vepsäläinen 1988, Pisarski and Vepsäläinen 1989).

The concept of competition hierarchy in ants is already well documented with examples of various interspecific interactions (e.g. Czechowski 1979, 1985, 1990b, 1999, 2000, Czechowski and Pisarski 1988, Czechowski and Vepsäläinen 2001, Savolainen and Vepsäläinen 1989, Savolainen *et al.* 1989, Savolainen 1990, 1991). As regards ants' ecological and behavioural interspecific relations in general Rezniková's (1983) book is an "encyclopedia" in its own.

This paper presents results of a study on the ecological interrelations between *Lasius psammophilus* Seifert and *Formica cinerea* Mayr, species that have not been studied in this respect [besides some of Gallé's (1991) observations]. Theoretically they are fairly competitive with each other, because they can inhabit the same types of habitat, and also co-occur frequently. In 2001, W. Cz. discovered a strange situation: an unusually large *Lasius psammophilus* nest complex was found in the immediate vicinity of a strong *Formica cinerea* colony, separated by less than one meter (Figs 2–4). This close neighbourhood persisted even a year later, with apparently no sign of mutual aggression. This situation gave birth to the following questions:

- To what extent does the activity of each of them overlap in time and space?
- Does the presence of *F. cinerea* influence the activity of *L. psammophilus*?
- Does the presence of *L. psammophilus* influence the activity of *F. cinerea*?
- Are there any direct interactions between the two species?

Summarizing: how is it possible for colonies of these two presumably competitive species to live together so close to each other? This study makes part of a larger research project on *F. cinerea*'s foraging strategies and foraging efficiency (Markó, in prep.).

STUDY AREA, SPECIES, MATERIALS AND METHODS

The studies were carried out at the site of W.Cz.'s preliminary findings (see above), in a complex of sand dunes near the village of Tvärminne on the Hanko Peninsula, S Finland (see Palmgren 1972, Keynäs 1996) (Fig. 1) in July 2001 and in June, July, and August 2002. The structure and succession of ant assemblages (Gallé 1991, Czechowski *et al.*, in prep.), as well as socially parasitic and competitive interspecific relations in ants (Czechowski and Rotkiewicz 1997, Czechowski 1999, 2000, 2001, Czechowski and Vepsäläinen 2001, Czechowski *et al.* 2002) had already been studied there. Altogether 30 ant species were recorded, and within these *L. psammophilus* (in Gallé 1991 called *L. alienus* Först. according to the taxonomy of that time) and *F. cinerea* belonged to the most abundant ones in respect of colony density.

Species

L. (Lasius) psammophilus is a species recently separated from the collective species «*L. alienus*» (Seifert 1992). It is an oligotope of dry thin grasslands, particularly those on sandy substratum, one of the most numerous ant species on dunes. It builds totally underground nests with entrances on the bottom of crater-like hollows; the vertical galleries reach down to 120 cm, the horizontal ones stretch over 10–30 cm under the surface (Seifert 1992). Colonies are monogynous, yet they often occupy multiple-nest systems composed of several interconnected nest units, each with its own entrance (see Brian *et al.* 1965, Nielsen 1972) (Fig. 5). Ants feed on honeydew of root aphids and also by scavenging and preying upon small insects. They are generally non-aggressive outside their nests. This species was not hitherto mentioned in papers dealing with competition hierarchy. By analogy to *L. niger* (L.) it may be considered a representative of an encounter species.

F. (Serviformica) cinerea is an oligotope of dry grasslands and forests that occurs exclusively in sun-exposed sandy habitats, from coastal and inland dunes to light pine forests. It builds deep and widespread underground nests (Pawlikowski and Pawłowicz 1984, Czechowski and Rotkiewicz 1997) similar in appearance, as well as their complexes, to those of *L. psammophilus* (Fig. 6) Colonies are monogynous or polygynous. The latter colony type can frequently develop into vast and very populous polydomous system (Lindström *et al.* 1996). It is an aggressive species living largely by predation and scavenging while also feeding on honeydew. The hierarchic status of the species has not been decisively cleared up. Pisarski and Vepsäläinen (1989) mentioned it among the examples of territorials, but Gallé (1991) considered it to be submissive. Some observations by Czechowski (1999) also point to, at least potential, territoriality in *F. cinerea*. For its ecology in Finland see Kilpiäinen *et al.* (1977).

Colonies

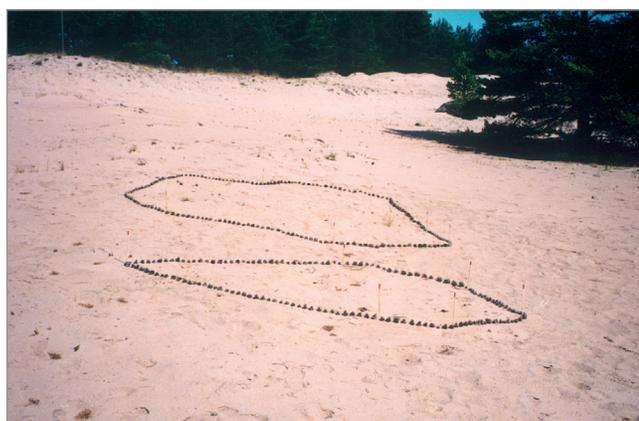
The boundaries of the *L. psammophilus* (and generally of *L. alienus* *sensu lato*) nests are hard to define, in the majority of the cases only entrance aggregations can be distinguished, and presumably these are made up of several interrelated nests or even colonies (Brian *et al.* 1965, Nielsen 1972, Gallé 1980, Gallé 1991, and the authors' own observations). Thus it is more appropriate to regard these formations as nest complexes, and not as single colonies. In our case two such *L. psammophilus* nest complexes were selected: nest complex A (Fig. 7a and c) was situated in the immediate vicinity of *F. cinerea* colony no. 25 (numbers referred to *F. cinerea* colonies are taken from B.M.'s unpublished material in order to keep the possibility of reference later on) (Fig. 7a–d), whereas nest complex B (Fig. 8) was the control, as the boundary of the nearest *F. cine-*



Fig. 1. Sand dunes at Tvärminne (photo W. Czechowski).



Fig. 2. Habitat of neighbouring nest complex A of *L. psammophilus* and colony no. 25 of *F. cinerea* (photo W. Czechowski).



Figs 3 and 4. Situation of nest areas of complex A of *L. psammophilus* (Fig. 3: on the right; Fig. 4: at the back) and of colony no. 25 of *F. cinerea* (Fig. 3: on the left; Fig. 4: in front), marked with pine cones (photo W. Czechowski, taken in 2001).



Fig. 5. Nest complex A of *L. psammophilus* (photo W. Czechowski, taken in 2000).



Fig. 6. Colony no. 25 of *F. cinerea* (a part) (photo B. Markó, taken in 2002).

rea colony lay 26 m away. The distance between nest complexes A and B was also 26 m.

The distance between nest complex A and colony no. 25 showed interesting variations: 90 cm in July 2001 (Figs 3 and 4), 136 cm on 29.06.2002, 133 cm on 10.07.2002 and 233 cm on 14.08.2002. Parallel to these

variations there were also changes in the number of entrances (Fig. 7a–d) and in the general structure of nest complex A. In July 2002 nest complex A showed the same compact core area as in 2001, however, some other entrances appeared at the upper part of the nest complex. The area covered by the entrances of the nest

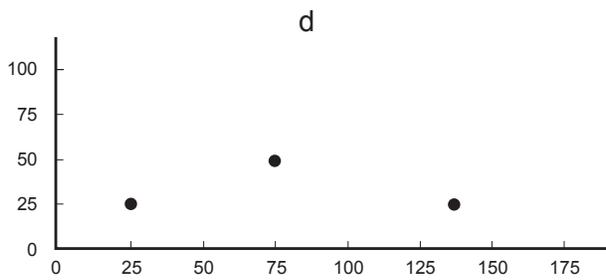
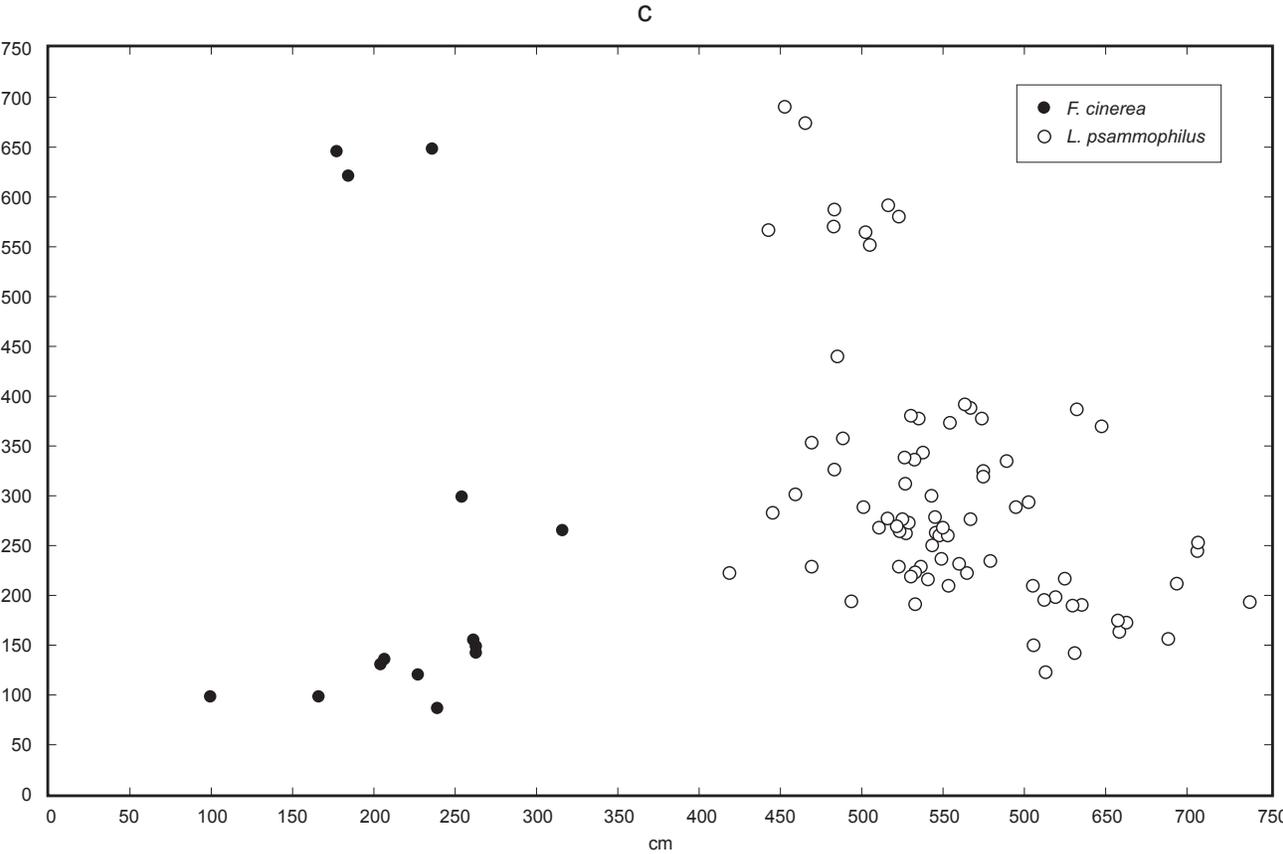
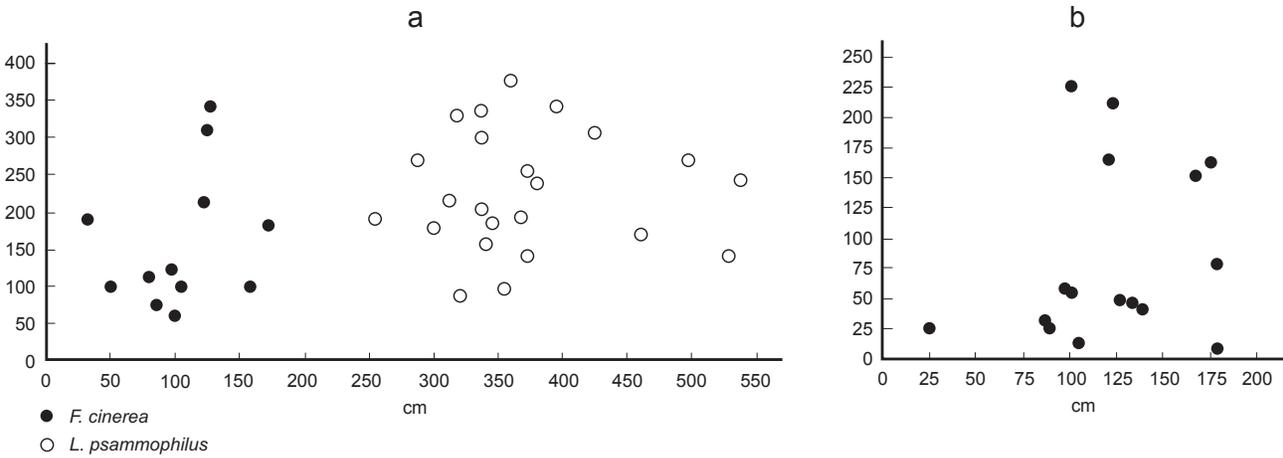


Fig. 7. Maps of complex A of *L. psammophilus*: (empty dots) and neighbouring *F. cinerea* colony no. 25 (filled dots): (a) both species in July 2001; (b) *F. cinerea* on 29.06.2002; (c) both species on 10.07.2002; (d) *F. cinerea* 14.08.2002. Distances are given in cm on the ordinates.

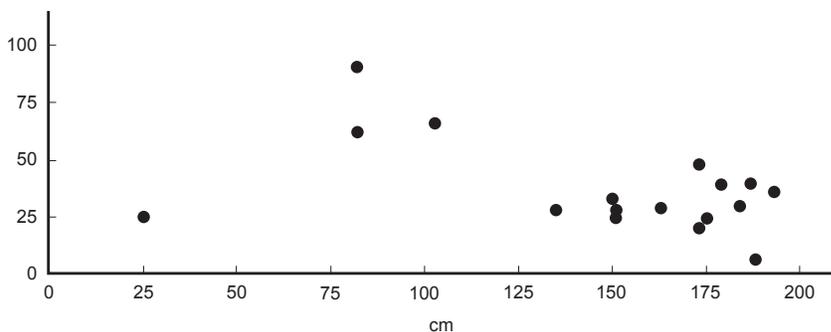


Fig. 8. Map of nest complex B of *L. psammophilus* on 22.07.2002. Distances are given in cm on the ordinates.

complex also expanded: from ca. 6.5 m² in 2001 it grew to ca. 8.64 m² in 2002. In the case of nest complex B the number of entrances was low, and the covered area was relatively small: ca. 1 m². However, the general size of *L. psammophilus* nest complexes was much similar to that of nest complex B, than to nest complex A.

Colony no. 25 of *F. cinerea* also showed major changes. The number of entrances changed to a great extent (Fig. 7a–d), as well as the colony’s area: from ca. 3.6 m² in 2001 to 2.5 m² in June and 2.7 m² in July 2002. The most relevant change occurred in August 2002, when the colony’s area was reduced to ca. 0.7 m². Such variations in the colony size are, however, not in the least rare in *F. cinerea* (Czechowski and Rotkiewicz 1997, Markó unpubl.).

Partial data regarding another *L. psammophilus* nest complex (C) neighbouring a *F. cinerea* colony (no. 8) was also used for this study (150 cm between the nearest entrances of *F. cinerea* and *L. psammophilus*). The distance between nest complex C and nest complexes B was ca. 400 m. Additional data regarding the spatial and temporal foraging pattern of *F. cinerea* and *L. psammophilus* individuals were also gathered around other *F. cinerea* colonies (nos. 1, 2, 3, 5, 11 and 24) besides the above-mentioned ones.

Activity observations

It is generally accepted that interactions among different ant species can be provoked by baiting experiments, and this method is appropriate for clarifying the position of each ant species in the community (Vepsäläinen and Pisarski 1982, Savolainen and Vepsäläinen 1988, Czechowski 1990a, Gallé 1991, Járdán *et al.* 1993, Gallé *et al.* 1998), because large and stable food sources are worth being defended, whereas small, easily-retrieved food is not necessarily so. It is also advisable to study the probability of interference in the lack of baits, e.g. the foraging pattern and the possibilities of interspecific contacts in order to get an accurate picture on the effect of baits. Thus eight observation plots were set up around each nest complex of *L. psammophilus* where the number of foraging

individuals was recorded for each ant species, as well as the frequency and type of aggressive interaction. The location of the first observation plot (see sign on Fig. 9) was selected randomly, using the Northern direction as reference. The other plots were selected according to the first. The plots were arranged systematically in two circles: inner (0.5 m from the border of the colony) and outer (1.5 m from the border of the colony), each circle containing four plots (Fig. 9).

The observations were carried out in three periods per day, each lasting 220 minutes. In each period each plot was verified in every 20 minutes for one minute, thus each period consisted of 11 observations. The first period began at 8⁰⁰ o’clock and ended at 11⁴⁰, the next one started at 12⁴⁰ and ended at 16²⁰, whereas the last one lasted from 17²⁰ till 21⁰⁰ o’clock. Because the data for each observation plot within each 20 minutes period are not statistically independent, the data were pooled over the eight plots for the activity analyses, and then averaged resulting in activities per one minute and one observation in the case of each colony. All activity data were log₁₀-transformed to normalize the data.

The first observation day was the so-called ‘nudum’ phase, when observations were carried out without baits. On the following day baits were put out in the centre of each plot. In order to avoid the effect of

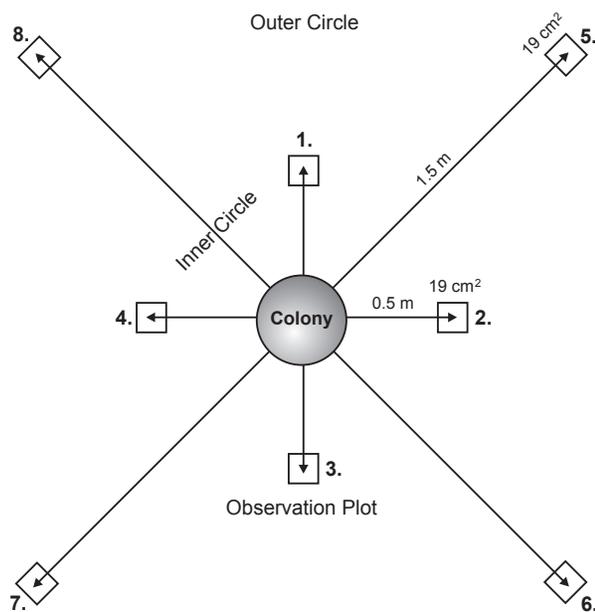


Fig. 9. The arrangement of rectangular observation plots around a colony. Distances of the plots are given from the border of the colony to the centre of each plot. The axis of the outer and inner circle crosses each other with 45° in the centre of the colony.

seasonal variation in food preferences the baits were made up of animal protein (tuna fish flakes), and carbohydrates (polyfloral honey). The bait patches (ca 3.5 cm diameter) were placed on matt green plastic plates with 9.5 cm diameter in the centers of the plots. At the beginning of each observation period new baits were put out 10 minutes before the first observation, and at the end of each period the baits were gathered.

It was previously observed that there could be fluctuations in the foraging activity of *L. psammophilus*. Thus *L. psammophilus* individuals could be seen active at the entrances, while almost no foraging individuals were present out of the nests. These individuals at the nest holes were generally engaged in cleaning activities, e.g. carrying out sand particles that had blocked the entrances during inactive periods. In order to obtain proper information on the species' activity individuals at four entrances were counted besides the inspection of the observation plots at nest complexes A and B. The entrances were selected such that they were close to the plots of the inner circle, and observations were carried out for one minute parallel to the inspection of these plots. Additionally the number of foraging *F. cinerea* and *L. psammophilus* individuals were also recorded outside the observation plots on the area of the *L. psammophilus* nest complex A and B for one minute in each observation period at the same interval of 20 minutes. The 'nudum' and bait observations were carried out on 23 and 24.07.2002 at nest complexes A and B.

The protocol presented above was also used in the case of *F. cinerea* colonies, only the inspection of the entrances was omitted. The 'nudum' observations at colonies nos. 25 and 24 were repeated five times periodically: on 11. (12. for the baits), 16., 21., 26., and 31.07.2002. The other *F. cinerea* colonies were also studied during June and July 2002.

At the beginning of each observation the temperature on the sand surface, and relative air humidity immediately above the ground were recorded both in sun-exposed, and in shaded patches. Digitron SP3R data printer was used for these measurements. If the majority of the observation plots were shaded the climatic values for these conditions were taken into account for the activity analyses.

RESULTS

Temporal interferences

Lasius psammophilus

The activity of *L. psammophilus* individuals was very low around nest complexes A and B in the 'nudum' phase. During altogether 264

minutes of recordings, only 2 and 3 individuals were observed in two vs. three plots at nest complexes A and B respectively. As comes to the foraging activity on the area of the nest complexes, altogether 6 and 35 foraging individuals were recorded at nest complexes A and B respectively (mean = 0.02 ind./min, SD = \pm 0.07 for nest complex A, and mean = 0.13 ind./min, SD = \pm 0.27 for nest complex B).

The activity at the entrances was more intense (Fig. 10): altogether 169 individuals were recorded (mean = 1.28 ind./entrance and per minute, SD = \pm 1.89) at nest complex A, and 468 individuals (mean = 3.54 ind./entrance and per minute, SD = \pm 4.29) at nest complex B. Only the activity of individuals at the entrances could be analyzed as a function of temperature and relative air humidity due to the low number of foragers. The number of individuals was pooled for each observation and averaged resulting in the number of individuals per entrance and minute in the case of each colony. The multiple regression analysis ($R^2 = 0.37$, $F = 10.28$, $p < 0.001$, $n = 33$ for nest complex A, and $R^2 = 0.18$, $F = 4.54$, $p < 0.05$, $n = 33$ for nest complex B) shows that the activity at the nest entrances is predicted by changes in the temperature on the sand surface. More specifically, the increase in temperature affected negatively the activity of *L. psammophilus*: (1) nest complex A beta = -0.62, $t = -4.4$ ($p < 0.001$); (2) nest complex B beta = -0.53, $t = -3.01$ ($p < 0.01$). Relative air humidity was less important: (1) nest complex A beta = 0.14, $t = 0.99$ (n.s.); (2) nest complex B beta = -0.25, $t = -1.43$ (n.s.).

Numbers of individuals active at the entrances were peaked (Fig. 10). Thus, the temperature range of the activity concentrated on relatively low values with a mean of 20.06°C (SD = \pm 2.44, $n = 637$), peaking at 17-

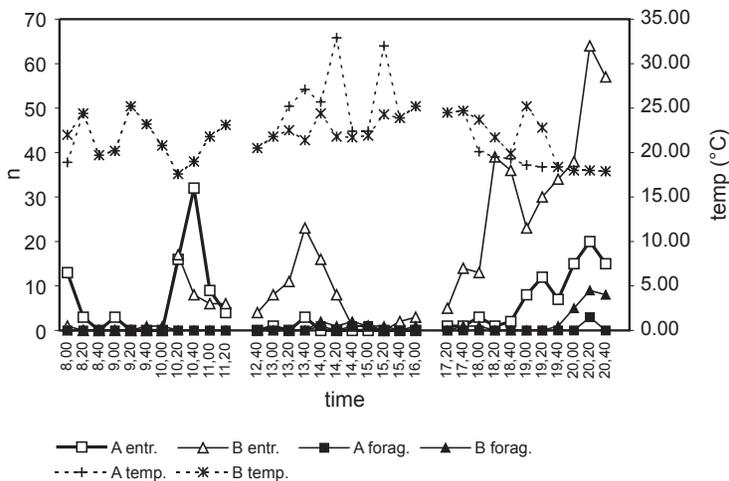


Fig. 10. Dynamics of *L. psammophilus* activity. Rectangles represent individuals at nest complex A, and triangles individuals at nest complex B. Filled symbols are for foraging individuals, empty symbols are for the activity at the entrances. Data for the entrances ($n = 4$) are pooled. Number of foraging individuals was pooled over every observation ($n = 33$), and every individual recorded on the territory of the colonies was taken into consideration.

18°C (Fig. 11), and on high relative air humidity values with a mean of 71.18% (SD = ± 13.5, n = 637) (Fig. 12). Individuals could start activity at the entrances during almost the whole day (Fig. 10), because decreasing temperature could be a signal for maintenance of nest entrances, as fine, dry sand collapses easily. Foraging activity began only at the end of the day.

The pooled data on foraging activity of *L. psammophilus* in observation plots around *F. cinerea* colonies and *L. psammophilus* nest complexes confirm the above findings on nest entrance activity. Altogether 26 foraging individuals were observed in plots (21 vs. 5 individuals around *F. cinerea* colonies and *L. psammophilus* nest complexes respectively), and the mean temperature value of the foraging activity was 20.84°C (SD = ± 5.31), whereas the mean relative air humidity value was 74.77% (SD = ± 16.55). Only data on individuals active at the entrances could be used further on for climatic comparisons owing to the low frequency of data on foraging *L. psammophilus*.

It was expected that the presence of baits would enhance the foraging activity. Indeed the number of foraging individuals increased considerably: altogether 270 individuals were observed on 10 baits around the studied *L. psammophilus* and *F. cinerea* colonies. Only the simple presence/absence of *L. psammophilus* on baits in every inspection was taken in consideration in order to exclude the effect of recruitment. Thus the mean temperature value reached 25.37°C (SD = ± 5.32, n = 114), whereas the mean relative air humidity was 53.26% (SD = ± 14.43, n = 114) in the presence of baits, which showed a shift to tolerance of higher temperatures (maximum value was 36.2°C vs. 27.1°C in ‘nudum’), and to lower humidity values (minimum value was 25% vs. 44% in ‘nudum’).

Formica cinerea

The data on *F. cinerea* foragers around 8 colonies show, that the changes in the temperature on the sand surface and the changes in the relative air humidity affected the activity of *F. cinerea* to a considerable extent (Table 1). The number of foraging individuals generally increased with temperature, whereas relative air humidity had mostly the opposite effect.

The number of foraging individuals in *F. cinerea* peaked around 9 and 10 o'clock, and between 16 and 18 o'clock during summer, when generally the temperature was between 30° and 40° (Fig. 11), while at the end of the day they seemed to minimize foraging activity. Mid-day, when the temperature could exceed 45° on the sand, was also more or less avoided. The

Colony	Date	Climatic factor	beta, t	R2, F
25	11.07	temperature	–	n.s.
		relative air humidity	–	
	16.07	temperature	-0.71, -1.09	0.19, 4.77*
		relative air humidity	0.49, 1.4	
	21.07	temperature	-0.17, -0.47	0.39, 11.38***
		relative air humidity	0.63, 2.45*	
	26.07	temperature	0.58, 3.98***	0.29, 7.72**
		relative air humidity	0.06, 0.25	
31.07	temperature	–	n.s.	
	relative air humidity	–		
24	11.07	temperature	–	n.s.
		relative air humidity	–	
	16.07	temperature	–	n.s.
		relative air humidity	–	
	21.07	temperature	-0.1, -0.27	0.21, 5.28*
		relative air humidity	-0.6, -1.51	
	26.07	temperature	–	n.s.
		relative air humidity	–	
31.07	temperature	–	n.s.	
	relative air humidity	–		
8	temperature	1.2, 2.96**	0.36, 10.26***	
	relative air humidity	0.65, 1.59		
11	temperature	1.26, 1.9	0.34, 9.15***	
	relative air humidity	0.68, 1.04		
3 (n = 22)	temperature	0.3, 0.68	0.28, 5.2*	
	relative air humidity	-0.3, -0.67		
5 (n = 22)	temperature	0.03, 0.1	0.6, 17.15***	
	relative air humidity	-0.77, -2.31*		
1 (n = 18)	temperature	–	n.s.	
	relative air humidity	–		
2 (n = 18)	temperature	0.15, 0.42	0.33, 9.06***	
	relative air humidity	-0.47, -1.26		

*p < 0.05, **p < 0.01, ***p < 0.001

Table 1. Relationship between the foraging activity of *F. cinerea* and climatic factors (temperature on soil surface and relative air humidity); multiple regression analysis, n = 33 in most cases. The number of individuals was pooled within each observation for each colony, and averaged, thus the number of individuals per observation plot and minute was taken into consideration.

temperature and relative air humidity ranges of foraging activity were analyzed in the case of colony no. 25, as the five full-day observations made possible a powerful assessment of the *F. cinerea*'s preferences (daily average = 0.29 ind. per plot and one minute, SD of the average = ± 0.12, n = 165, total no. of individuals = 336). The mean temperature value of the species' activity was 33.22°C (SD = ± 6.93, n = 336) and the mean relative air humidity value was 35.73% (SD = ± 20.62, n = 336).

Formica cinerea vs. Lasius psammophilus

The comparison of the temperature and relative air humidity ranges of *L. psammophilus* individuals

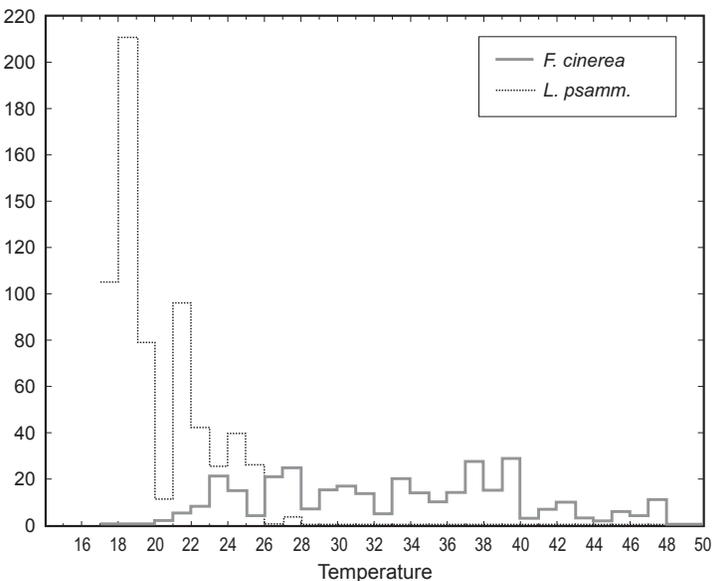


Fig. 11. The temperature range of the activity in *L. psammophilus* (individuals at the entrances at nest complexes A and B) and the same in *F. cinerea* (foraging individuals at colony no. 25).

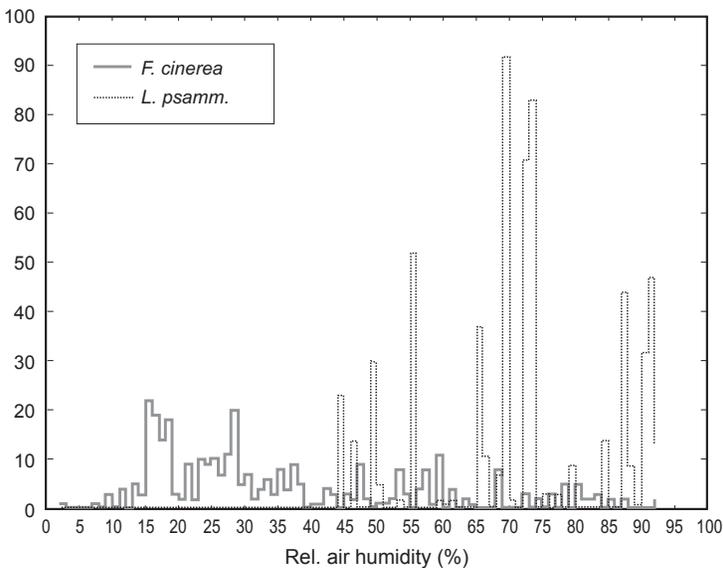


Fig. 12. The relative air humidity range of the activity in *L. psammophilus* (individuals at the entrances at nest complexes A and B) and the same in *F. cinerea* (foraging individuals at colony no. 25).

in the entrances and that of *F. cinerea* foragers shows that indeed *F. cinerea* preferred significantly warmer periods (Mann-Whitney U-test $z = -24.52$, $p < 0.000$, $n_{Lps} = 637$, $n_{Fc} = 336$) (Fig. 11) and lower relative air humidity (Mann-Whitney U-test $z = -20.49$, $p < 0.000$, $n_{Lps} = 637$, $n_{Fc} = 336$) (Fig. 12).

The effect of *F. cinerea*'s presence on the activity of *L. psammophilus* was analyzed by comparing the activity of *L. psammophilus* individuals in the entrances at nest complex A (near colony no. 25 of *F. cinerea*) with

the activity at nest complex B (control, without *F. cinerea* neighbours). The activity of *L. psammophilus* individuals showed the same pattern at both nest complexes (Pearson $r = 0.53$, $p < 0.001$, $n = 31$), but the number of individuals at nest complex B (control) was higher, than at nest complex A (Fig. 10, Mann-Whitney U-test $z = -2.41$, $p < 0.05$, $n_{1,2} = 33$, two-tailed).

The comparison of the activity of *F. cinerea* individuals at colony no. 24 (control, without *L. psammophilus* nest complex in the vicinity) with the activity at colony no. 25 (neighbouring nest complex A of *L. psammophilus*) allowed us to assess the effect of the vicinity of *L. psammophilus* nest complexes on the activity of *F. cinerea*. In the majority of the cases there was no significant correlation (Table 2) between the dynamics of the colonies on the same day. The restricting (lower activity of *F. cinerea* at colony no. 25) or the enhancing (higher activity of *F. cinerea* at colony no. 25) effect of *L. psammophilus* neighbourhood was not clearly supported by the Mann-Whitney U-test (Table 2). The changes in the sign of differences between the activities of *F. cinerea* individuals at these two colonies clearly suggested the effect of other factors.

Date	Relationship of means	Mann-Whitney U-test, z	Correlation, Pearson r
11.07	>	-2.51*	0.5**
16.07	>	-3.01**	0.46**
21.07	>	-1.77	0.23
26.07	<	-0.76	0.19
31.07	<	-4.02***	0.07

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 2. Comparison of the daily activity of *F. cinerea* foraging individuals at colonies no. 25 (neighbouring nest complex A of *L. psammophilus*) and no. 24 (control) in 'nudum' phase ($n_{1,2} = 33$, two-tailed tests). Relationship: >/< – more/less foragers at colony no. 25 than at colony no. 24.

Spatial interferences

Lasius psammophilus

A single *L. psammophilus* individual was recorded in observation plots around *F. cinerea* colony no. 25 (in an outer plot at 20⁰⁰) during the five observation days in 'nudum' phase. This suggests that *L. psammophilus* rarely enters the area of the *F. cinerea* colony regardless of the vicinity. Data on the presence of *L. psammophilus* in observation plots around other *F. cinerea* colonies in 'nudum' phase ($n = 20$) confirm that individuals rarely forage close to *F. cinerea* nests. The majority of observations ($n = 15$) came from the plots of the outer circle.

Consequently *L. psammophilus* individuals were observed mainly on baits of the outer circle around colonies of *F. cinerea*. Out of ten baits, which were found by *L. psammophilus* individuals, seven were on the outer circle. This bias also stands in the case of the dominated baits: four baits out of the total of five dominated clearly by *L. psammophilus* were on the outer circle.

The baiting experiments offered interesting results at nest complexes A and B: only one *L. psammophilus* individual was observed on bait no. 1 of nest complex A, and no forager was found on the baits around nest complex B. This outcome was unexpected due the fact that previous baiting experiments around colony no. 25 resulted in the recruitment of *L. psammophilus* to bait no. 5 (Table 3). It is also true, that this bait was situated in the immediate vicinity (8 cm) of a *L. psammophilus* entrance.

<i>F. cinerea</i> colony	Bait no.	Distance from <i>L. psammophilus</i> entrance (cm)	Maximum no. of foragers
25	5	8	120
24	3	95	100
5	8	187-188	52
8	8	150	43
8	5	4	14

Table 3. Baits monopolized by *L. psammophilus* around *F. cinerea* colonies: the distance between the bait and the *L. psammophilus* entrance where foragers came from, and maximum number of foragers recorded.

Naturally the foraging area of *L. psammophilus* could extend in the presence of baits. Foraging individuals were observed only on nine plots around *F. cinerea* colonies in 'nudum' phase, whereas foragers were recorded on 11 baits afterwards. By considering the fact that only five baits coincided with previous observations it could be concluded that fortuitousness was an appropriate characteristic of the species' foraging strategy. This was supported if taking account of the variation in the distances between the baits on which recruitment was observed and the entrances where foragers came from (Table 3): from a few centimeters to almost 2 meters. On the basis of this variation one would expect that *L. psammophilus* foragers should have found almost all baits around nest complexes A and B. It was rather strange, that bait no. 3, at colony no. 24, was almost twice as far from the *L. psammophilus* entrance as bait no. 6 (45 cm away), and *L. psammophilus* foragers did not discover this latter one.

Formica cinerea

The basic rules regarding the *F. cinerea* foragers' distribution around their colonies are also worth of being analyzed. The number of individuals was gener-

ally decreasing with distance from the colony (Table 4), which resulted in significant differences between observation plots even at distances as small as 0.5 vs. 1.5 m from the colony. These differences were emphasized in the case of colony no. 25 and no. 8. This pattern persisted in the presence of baits, too (Markó, in prep.).

Colony, Date	Inner vs. outer		
	Relationship	Mann-Whitney U-test, z (n = 33)	
near <i>L. psammophilus</i> nest complexes			
8	>	-6.12***	
25	11.07	>	-3.29**
	16.07	>	-3.36**
	21.07	>	-5.25***
	26.07	>	-4.33***
	31.07	>	-2.71*
without <i>L. psammophilus</i> nest complex neighbours			
1 (n = 18)	>	-5.01***	
2 (n = 18)	<	-1.98*	
3 (n = 22)	<	-1.85	
5 (n = 22)	>	-0.33	
11	>	-2.47*	
24	11.07	>	-0.52
	16.07	>	-1.02
	21.07	>	-1.08
	26.07	>	-4.33***
	31.07	>	-3.88***

*p<0.05, **p<0.01, ***p<0.001

Table 4. Comparison of the number of *F. cinerea* foragers in the inner and outer observation circle (Mann-Whitney U-test, n = 33, two-tailed). Relationship: >/< - more/less foragers in the inner than in the outer circles.

F. cinerea was observed on several baits in the baiting experiments around nest complex A, and strong recruitment developed to the bait closest to the *F. cinerea* colony (bait no. 7). The presence of *F. cinerea* foragers was more or less stable almost exclusively on closer baits, nevertheless only bait no. 7 was constantly exploited (Table 5).

Bait	1	2	3	4	5	6	7	8
Distance from <i>F. cinerea</i> colony	distant	distant	close	close	distant	distant	close	close
Constancy	0	0.06	0.36	0.18	0	0.51	0.94	0.09
Mean	0	0.06	0.52	0.18	0	0.88	17.57	0.06
Max. no.	0	1	2	1	0	4	37	1

Table 5. Presence of *F. cinerea* foragers on baits close or distant to nest complex A of *L. psammophilus* during baiting experiment around nest complex A. Constancy = no. of occurrences/total no. of observations (= 33).

Formica cinerea vs. Lasius psammophilus

Differences in the numbers of *F. cinerea* foragers could be showed when analyzing the distribution of *F. cinerea* individuals around *F. cinerea* colonies with

L. psammophilus nest complexes in their vicinity and without such neighbours: the number of *F. cinerea* individuals was always lower in the outer circle at colony no. 25 and no. 8 (neighbouring nest complex A and C respectively), which did not stand for the control colonies in every case in 'nudum' phase (Table 4).

It was also worthwhile to check whether there could be differences in foraging pattern between plots at small versus large distance from *L. psammophilus* nest complexes in the case of *F. cinerea* colonies no. 25 and no. 8 in 'nudum' phase. The number of close and distant plots was four (2 on outer and 2 on inner circle in every case) and the data were pooled for the analysis. The results confirm that indeed there were significantly less foragers on plots close to *L. psammophilus* nests than in plots far away in the majority of the cases (in four out of five observation days $z < -3$, $p < 0.01$ at colony no. 25, and $z = -3.6$, $p < 0.01$ at colony no. 8; $n = 33$).

Consequently *F. cinerea* foragers were rarely observed on the area of nest complex A of *L. psammophilus* in 'nudum' phase. Generally the average of the daily means of foragers per minute over six days of observation on the whole territory of nest complex A was lower (mean = 0.14, SD = ± 0.13, $n = 6$, min = 0, max = 0.24) than the five days average (on 23.07 only nest complex A was studied) of the daily means of foragers on observation plots at colony no. 25 (mean = 2.33, SD = ± 1.01, $n = 5$, min = 0.78, max = 3.39) in 'nudum' phase. On this basis the hypothesis that the vicinity of *F. cinerea* could restrict the activity in nest complex A becomes very unlikely.

Colony no. 8 was in the vicinity of colony C, and two observation plots on the outer circle were situated on the area of colony C. The number of observed *F. cinerea* foragers was also very low (as in the case of colony no. 25): 3 and 6 individuals respectively on both observation plots during all day of 'nudum' observations.

The above-presented findings seemed to persist even if baits were present. In the cases of both colonies of *F. cinerea* (25 and 8) that were situated in the vicinity of *L. psammophilus* nest complexes the baits that were closer to the *L. psammophilus* nest complexes were less efficiently monopolized by *F. cinerea* than baits far away (Mann-Whitney U-test $z = 4.42$, $p < 0.01$, $n = 33$ for colony no. 25, and $z = 5.94$, $p < 0.01$, $n = 33$ for colony no. 8). The baiting experiments made specifically around nest complex A emphasize these results. *F. cinerea* were recorded mostly on baits neighbouring their colony (Table 5), and recruitment process was observed only on the closest bait (no. 7) laying only 23 cm away from the nearest *F. cinerea* entrance.

Foraging success and interactions

Baiting experiments around *F. cinerea* colonies showed that indeed *F. cinerea* was more successful in finding and monopolizing such food sources in the areas inhabited by it (Table 6). However, the recruitment system of *L. psammophilus* was more successful: the maximum number of foragers present on the baits could be higher than that of *F. cinerea* (Fig. 13). The superior communication system of *L. psammophilus* made possible that one successful forager could attract a huge number of nestmates almost irrespective of the distance of the food source.

The few aggressive interactions (Table 6) were generally won by *F. cinerea*. There was also evidence for the opposite event, although this occurred only

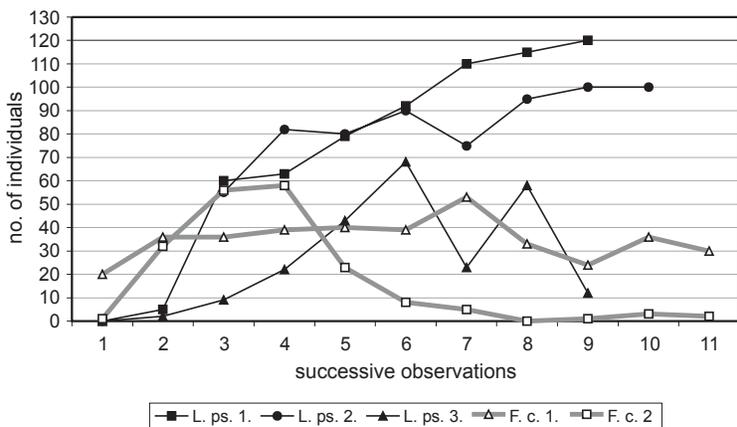


Fig. 13. Numbers of foragers on baits (*L. psammophilus*: 1 – colony no. 25, bait no. 5, evening, 2 – colony no. 24, bait no. 3, evening, 3 – colony no. 24, bait no. 3, forenoon; *F. cinerea*: 1 – colony no. 8, bait no. 3, forenoon, 2 – colony no. 24, bait no. 4, forenoon).

once. However, generally *F. cinerea* foragers would not intrude when *L. psammophilus* had already monopolized the given bait by mass recruitment. In these cases almost no interactions occurred.; In some cases *F. cinerea* tapped the abdomen of a *L. psammophilus* with its antennae, then it ran away almost immediately.

The aggressive behaviour of *F. cinerea* towards *L. psammophilus* was only once observed in the lack of

Type of interactions	Absolute frequency of observations on baits (no. of baits)	No. of monopolized baits	Absolute frequency of co-occurrences (no. of baits)	Absolute frequency of peaceful co-occurrences	Driven away by the rival (no. of specimens)	Interspecific fights (no. of engaged specimens)
<i>L. psammophilus</i>	114 (10)	5	13 (8)	9	8	2
<i>F. cinerea</i>	1453 (78)	74			1	5

Table 6. Presence of both species on baits around *F. cinerea* colonies and frequency of different types of interactions.

baits: the conflict arose because of a "dispute" over an item of prey. One *F. cinerea* forager on its return to its nest accidentally fell in a *L. psammophilus* entrance with its prey (a spider) at colony no. 3 on 10.07.2002. The *L. psammophilus* individuals attacked the *F. cinerea* forager at once. A few other *cinerea* foragers were clearly alerted, and while some of them tried to help, others returned to the nest. In less than 30 minutes a diffuse raid of *cinerea* was heading for the *L. psammophilus* entrance. The battle was unsuccessful because *F. cinerea* workers could hardly get a grip on the much smaller *L. psammophilus*, whilst the latter could successfully bite the adversaries' legs and antennae. Finally sand particles blocked the entrance, and just a few *F. cinerea* workers remained there guarding. The *L. psammophilus* entrance was still blocked on 18.07.2002, there were no signs of any kind of activity. Thus *F. cinerea* won the battle in a strange way by forcing *L. psammophilus* to "give up" the entrance at least for a while. It is worth to mention that this entrance was 567 cm away from the *F. cinerea* entrance where the raid came from. All things considered it is reasonable to assume that if conflicts had occurred between colony no. 25 and nest complex A, or between colony no. 8 and nest complex C, then *L. psammophilus* would have been forced to move farther from the neighbouring *F. cinerea* colony at short notice, or at least to cease the activity in some of the entrances for quite a while.

DISCUSSION

Species similar in one or two ecological characteristics should be dissimilar in others as a rule (Savolainen 1991). The probability that two ant species which display similar habitat requirements and population characteristics can live close to each other is low. The occurrence of such situation obviously raises some questions on the nature and possible ways of coexistence. There are a lot of known facts regarding interspecific competitive exclusion in ant assemblages, especially in relations between territorial and subordinate species. For instance wood ants (the subgenus *Formica* s. str.) destroy *Camponotus* colonies (Savolainen and Vepsäläinen 1988, Czechowski 1990b and unpubl.), whilst an artificially colonized *Formica polyctena* Först. eliminates even submissive species from the vicinity of its colony within a radius of at least 2–3 m (Czechowski 1990b). Rosengren (1969) reports the lack of other ant species' nests within the colony area of territorial *F. (Serviformica) uralensis* Ruzs. *Lasius niger* nests only in areas rarely searched by *F. polyctena*, where encounters between the species hardly occur (Mabelis 1984). Pisarski (1982) shows similar relation between *L. niger* and *F. (Coptoformica) exsecta* Nyl. So, what makes *F. cinerea*, a species known for its aggressiveness, let *L. psammophilus* prosper at a some-

times-shorter distance than one meter? If this happens, then obviously there must be some differences in the two species, which make possible the coexistence.

In the case of *Formica exsecta* and *Camponotus ligniperdus* (Latr.) it is known that the differences in daily activity rhythms could allow them to nest very close to each other (Czechowski and Pisarski 1988). Thus it is not surprising, that temporal interferences are minor between *F. cinerea* and *L. psammophilus*, which allow them to live close to each other. The basic factor seems to be the different reaction to the changes in temperature and air humidity. *L. psammophilus* seems to prefer cloudy (low temperature), and humid periods, whereas *F. cinerea* is active in sunny, dry periods mostly, e.g. the middle part of the day. Nevertheless the presence of ephemeral but large food sources can shift the activity range of *L. psammophilus* toward that of the *F. cinerea*'s (higher temperature and less humidity). Consequently the possibility of interference should be higher in the presence of such food sources, which, however, under natural conditions are not too frequent on sand dunes. Other studies (Gallé 1991) also support the lack of major activity overlaps between *F. cinerea* and *L. psammophilus*.

When comparing the activity of *L. psammophilus* colonies in the presence and in the absence of *F. cinerea* neighbours we found, that although there were differences in the number of individuals, the presence of *F. cinerea* colonies did not seem to affect the activity of *L. psammophilus*. Baiting experiments also supported this, as *F. cinerea* showed little interest in baits located on the territory of *L. psammophilus* nest complexes. On the other hand the presence of *L. psammophilus* did not influence the activity of *F. cinerea*. Basically the significant decrease in the number of *F. cinerea* foragers with distance from their colony allowed for a lower probability of interference with foragers of the rival species. Parallel to this, less *F. cinerea* foragers were found in the vicinity of *L. psammophilus* nest complexes than on plots distant to them. This suggests that close proximity to allospecific colonies could have evolved exactly because of the initially little interest of *F. cinerea* foragers in the area inhabited by *L. psammophilus*. *F. cinerea* raid on a *L. psammophilus* colony lying more than 5 meters away from colony no. 3 (see Results) clearly demonstrates that in the event of a conflict *F. cinerea* would not hesitate to intervene aggressively regardless of distance.

The exploitation of the baits by *F. cinerea* around nest complex A showed the same pattern as observed in 'nudum' (control condition without bait). Additionally the lack of both species on baits around nest complex B, suggests that the hypothesis according to which *L. psammophilus* foragers would not appear on baits around nest complex A because of the vicinity of *F. cinerea*, can also be rejected, also because recruit-

ment of *L. psammophilus* was observed on other baits around *F. cinerea* colonies.

The changes in the structure of two neighbouring big colonies (nest complex A and colony no. 25 of *F. cinerea*), show that *L. psammophilus*' expansion to even a closer distance from its neighbour is possible, due to the high variation in the spatial structure of the *F. cinerea* colony. As generally the galleries of these nests can be present in areas where there are no entrances, the problem of nest area size must be handled carefully. Variations in the structure of *F. cinerea* nests or nest complexes are not in the least unusual (Czechowski and Rotkiewicz 1997, Markó, unpubl.), and the observation regarding the disappearance of the majority of entrances at colony no. 25 should not be regarded as the sign of the colony's tragic decline, but as the result of several factors, e.g. frequent rains blocking the less active entrances.

Differences in foraging strategies can also account for the coexistence of species (Savolainen 1990, 1991). Chance is a very characteristic property of the foraging strategy of *L. psammophilus*. Food sources are not discovered by systematic search carried out by several individuals during the day, as it generally happens in *F. cinerea*. In contrast to this chance handicap *L. psammophilus* is more efficient in recruiting than *F. cinerea*. Its strategy of mass recruitment also serves as a passive defense system, as *F. cinerea* foragers rarely attack *L. psammophilus* individuals gathered on baits. Gallé (1991) reports the same behaviour from Tvärminne. Nevertheless it is clear that *F. cinerea* is more successful than *L. psammophilus* in discovering and monopolizing large food sources. Seemingly there is a contradiction with the observations of Gallé (1991) who reports that *L. psammophilus* detects the majority of the baits at Tvärminne, and not *F. cinerea*. Gallé's (1991) baiting experiments were, however, carried out in an area, which was dominated by *L. psammophilus* — 3.24 nests/100 m² for *L. psammophilus* vs. 0.6 nest/100 m² for *F. cinerea* — which predicted the success of *L. psammophilus*. On the other hand our baiting experiments were carried out mainly on areas inhabited by *F. cinerea* colonies, with the exception of the nest-complex B of *L. psammophilus*, which, yielded no discoveries at all by *L. psammophilus*, emphasizing once again its foraging handicaps. Gallé (1991) observes co-occurrences on baits in only 26 cases of the total of 327 observations. He reports that in the majority of the cases *F. cinerea* is "peacefully" excluded by *L. psammophilus* (see explanation above), and that only two cases of aggression were observed, one by *L. psammophilus* towards *F. cinerea*, and another one by *F. cinerea* towards *L. psammophilus*.

There is no information regarding the differences in the size of prey retrieved by individuals of the two types of colonies, but naturally we would expect that

L. psammophilus foragers are restricted to collecting smaller prey in the neighbourhood of *F. cinerea* colonies just because the presence of aggressive *F. cinerea* foragers push them to select for more rapidly and easily retrievable prey. The same is reported in the case of *F. polyctena* and *F. fusca* species pair (Savolainen 1991), where the latter is generally forced to select for smaller prey size in the presence of the aggressive species.

The coexistence of the two species on the sand dunes is also assured by differences in their habitat requirements. Usually *L. psammophilus* can be found everywhere in sandy areas, however, its density decreases from bare sand to vegetated areas (Gallé 1991, Járdán *et al.* 1993, Gallé *et al.* 1998). *F. cinerea* can be found mostly in sparsely vegetated areas (Gallé 1991, Gallé *et al.* 1998) in the vicinity of pine trees, which are generally visited for their aphid colonies obligatory for the development of bigger colonies. An unusual support of *L. psammophilus* against the *F. cinerea*'s overwhelming presence is the presence of *Formica sanguinea* Latr., which often destroys the *F. cinerea* colonies by raiding for slaves (Czechowski and Rotkiewicz 1997, Czechowski 1999, 2001 and unpubl.). *F. sanguinea* could be the cause of *F. cinerea* lacking in many areas of the sand dunes (Czechowski, unpubl.), areas that then can easily be colonized by *L. psammophilus*.

It is not easy to determine which competitive category these species fit in. In a few cases aggression towards *F. cinerea* by *L. psammophilus* can be observed (Gallé 1991 and present study), which places *L. psammophilus* among the encounter species according to Pisarski and Vepsäläinen's (1989) classification. Nevertheless in the majority of the cases *F. cinerea* clearly dominates, and our observed raid on a *L. psammophilus* colony proves once more its superiority. *L. psammophilus* seems to be flexible in its behaviour: when present in low numbers it behaves more like a submissive species giving up the food source easily, but when it becomes numerically strong it can act like an encounter species, defending the bait even against the twice-bigger, physically uncomparatively stronger and very aggressive *F. cinerea*. Being in all likelihood an encounter species, *L. psammophilus* most probably, occupies a lower position in the competition hierarchy than another encounter species, *L. niger*. As Brian *et al.* (1965) shows, *L. niger* keeps *L. alienus* sensu Förster (i.e. *L. psammophilus* or one of its sibling species) underground when these two species co-occur.

F. cinerea's rank was also debated: it was considered to be territorial (Pisarski and Vepsäläinen 1989), and submissive (Gallé 1991, Gallé *et al.* 1998) as well. Our results neither confirmed nor contradicted territoriality of this species. What is only obvious on the basis of the present study is that *F. cinerea* is not a submissive species, but under certain circumstances it also lets

other species (as *L. psammophilus*) dominate the baits. All in all the present study shows that *F. cinerea* seems to be an encounter species with territorial tendencies in the habitat (sand dunes) and the region (S Finland) studied. Pure territorial tendencies would be in contradiction with our observations of *L. psammophilus* not only nesting so close to *F. cinerea* colonies, while also (what is more significant) successfully monopolizing baits around these colonies. Of course, this does not exclude the possibility, and even speaks in advocacy of it, that *F. cinerea* is fully territorial in habitats and regions especially suitable for it, i.e. in habitats where colonies reach their enormous sizes (eg. in a young pine forest in Chernigov Province, Nezhyn Distr., N Ukraine; Radchenko, pers. comm.).

In ants the hierarchies are based mainly on behavioural differences in communication and aggressiveness, which can be regarded as a function of colony size and consequently of forager density (Savolainen *et al.* 1989). The communication system of *L. psammophilus* is clearly superior to that of *F. cinerea*, but *F. cinerea* dominates in the density of its foragers, and also in its aggressiveness. The problem of competitive rank should, however, be handled carefully as every species displays a plasticity of some extent, which is related to the colony cycle — small, incipient colonies are generally submissive, and as the colony grows its position becomes stronger — as well as to other external factors, e.g. the foragers' distance from the colony, and environmental conditions.

Though it is generally accepted that species from a lower rank can live together with a species from a higher rank (Vepsäläinen and Pisarski 1982, Pisarski and Vepsäläinen 1989, Savolainen *et al.* 1989, Gallé 1991, Gallé *et al.* 1998), in this case the shortage of resources (food and nesting sites) — which generally characterizes sand dunes — should call for stronger competition even between species of different ranks (Gallé *et al.* 1998). The exceptional size of our two *L. psammophilus* colonies neighbouring *F. cinerea* colonies is clear evidence supporting the possibility of coexistence (Savolainen 1990). The different activity and foraging strategies can allow these species to coexist even at otherwise "inadmissible" distances.

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