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Inter- and intraspecific competitive relations in *Camponotus ligniperdus* (LATR.) (*Hymenoptera, Formicidae*)

[With 3 Tables and 7 Figures in the text]

Abstract. The paper presents results of observations and experiments on the interspecific (mainly with *Formica exsecta* NYL. and *F. fusca* L.) and intraspecific competitive behaviour in *Camponotus ligniperdus* (LATR.). The status of this species in the hierarchical system within ant communities is discussed. The investigations were carried out in the Tvärminne Archipelago (southern Finland) in 1981 and 1983 and in the Gorce Mts. (the Western Carpathians; southern Poland) in 1985.

INTRODUCTION

The paper is a result of observations on the competitive behaviour of *Camponotus ligniperdus* (LATR.) towards ants of other species (and vice versa) and towards alien representatives of the same species. The present study is also an attempt to determine the territorial relations of *C. ligniperdus* ants, and their status in the interspecific dominance hierarchy of communities of *Formicidae*. The investigations were carried out in 1981 and 1983 on the island Joskär in the Tvärminne Archipelago within the Tvärminne Zoological Station, the Helsinki University (southern Finland) and in 1985 in the Gorce Mts. (the Western Carpathians) near the village Ochotnica Górna (southern Poland).

BIONOMIC CHARACTERISTICS OF THE SPECIES

The position of a given ant species in the interspecific dominance hierarchy depends on the level of its social organization and on a complex of psycho-physical features indispensable to the general vital efficiency of individuals

and colonies. Several-year-old colonies of *C. ligniperdus* have about 2,000 individuals (KRZYSZTOFIAK, unpublished data). The abundance of older, mature colonies may be estimated at over a dozen thousand workers. This gives the species an average position in the ant world. Generally, colonies of *C. ligniperdus* are monogynic, though cases of oligogyny have also been recorded (HÖLLDOBLER 1962). The intercolonial polymorphism, and polyethism which is connected with it are highly developed. Workers of the minor type are first of all responsible for the tasks inside the nest. Outside tasks are carried out by individuals of the media and major types and the latter usually stick to their defensive function only (KIIL 1934). The proportions of particular forms are a function of the age of a given colony — the older it is the greater is the percentage of big individuals (KRZYSZTOFIAK, unpublished data).

As a result of their size, *C. ligniperdus* ants possess great physical strength. In a single combat they can kill, with one snap of the mandibles, any ant they come across. Their abilities in this respect were exemplified by the composition of a cemetery-refuse ground belonging to one of the colonies of this species from the island Joskär. The nest was within the territory of *Formica polyctena* FOERST. near a foraging route of these ants. In the cemetery (found in July 1981), apart from 22 dead workers of *C. ligniperdus*, there were remains of the following invertebrates: 25 *Coleoptera*, 20 *Diptera*, 17 *Aranei*, 7 *Hymenoptera* (without ants), 5 *Hetcroptera*, 5 *Lepidoptera* or *Symphyta* (caterpillars) and 625 ☿☿, 2 ♀♀ *Formica polyctena* FOERST., 560 ☿☿, 8 ♀♀, 35♂♂ *Myrmica* sp. (*M. ruginodis* NYL., *M. scabrinodis* NYL. *M. lobicornis* NYL.), 46 ☿☿ *Formica fusca* L., 20 ♀♀, 10♂♂ *Lasius* sp., 27 ☿☿ *L. flavus* (FABR.), 17 ☿☿ *L. niger* L., 1 ☿ *Formica truncorum* FABR., 1 ☿ *Tetramorium caespitum* (L.) and 1 ☿ *Leptothorax acervorum* (FABR.). Almost 95 per cent of the prey of this colony were ants of other species! Thus, under certain circumstances *C. ligniperdus* is found to be an almost specialized myrmecophage. As a rule, these ants prey on animals incomparably small and weak in relation to their own potential abilities: on hymenopterans from the family *Braconidae*, bugs (*Heteroptera*) and hemipterans (*Homoptera*), dipterans from the families *Bibionidae*, *Culicidae* and *Scatophagidae*, and harvestmen (*Opiliones*) (KRZYSZTOFIAK, unpublished data). Most probably, while nesting in the territory of *F. polyctena* and within an area penetrated intensively by these ants, *C. ligniperdus* foragers had hardly any chances to find their usual prey. In such a situation, other ants, especially *F. polyctena*, were the only available food.

Under normal conditions, in their contacts with other ants *C. ligniperdus* workers seem to avoid using of their physical advantage. On the contrary, in certain situations they behave quite helplessly. For instance, they fall victim to definitely smaller ants which steal their prey. On the island Joskär it was observed several times that a *C. ligniperdus* worker carrying its prey was followed by an ant of *L. niger* very closely. In one of such cases, the *C. ligniperdus* forager (of the media type) dropped for a while the insect it was carrying and, standing beside it, began to clean the antennae. At that moment the accompanying

L. niger ant immediately snatched the prey from under the very mandibles of the *C. ligniperdus* worker and ran away.

In the Gorce Mts., there were recorded a few cases of *C. ligniperdus* offspring being stolen from their nests by ants of *Formica cunicularia* Latr. That happened in cases when *C. ligniperdus* nests situated under stones were accidentally uncovered. *F. cunicularia* workers that happened to be nearby ran into the nest at once and, never attacked, immediately carried larvae out of the nest from among the swarm of panicky *C. ligniperdus* ants.

In the bionomics of *C. ligniperdus* there are some features which point to a primitive character of the species. Their system of communication between individuals is developed poorly and therefore the degree of their cooperation is low. This definitely weakens the position of *C. ligniperdus* in relation to other species. Their poor food recruitment and the subsequent low efficiency in their utilization of food sources will be discussed in detail later. In *C. ligniperdus*, lack of cooperation is also manifested in their way of fighting. Some fights (always defensive) were recorded on the island Joskār and there *Formica exsecta* Nyl. was the opponent of *C. ligniperdus*. The behaviour of fighting *C. ligniperdus* workers was characterized by complete lack of help for individuals in danger. The fact that a soldier was caught by *F. exsecta* ants evoked no reaction in its nestmates present nearby. It happened several times that an able-bodied soldier which encountered a group of *F. exsecta* killing another *C. ligniperdus* individual merely touched the enemies (and their victim) with its antennae and, if they did not move, went away. It was, in some extent, in contrast with the war tactics of *C. ligniperdus*. Now, soldiers worked in pairs. Generally, two individuals left the nest, together they went to the battlefield or to the patrolled area and there too they moved side by side (at a distance of a few or over a do-

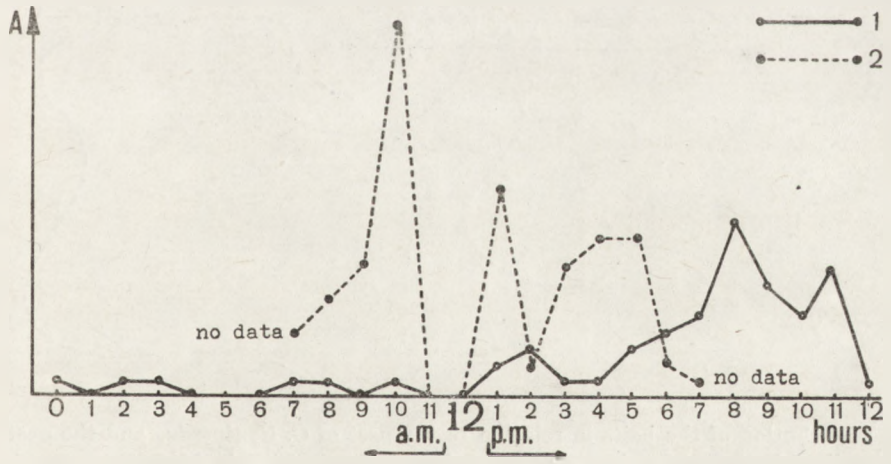

Fig. 1. Circadian rhytms of the activity of *C. ligniperdus* (1) (after Krzysztofiak, unpublished data) and *Formica exsecta* (2) (after Pisarski 1982a) (A — intensity of the activity measured by the number of individuals going out to forage).

zen centimetres). After one of them had been caught by the enemy the other went on with its task alone, without any visible change in its behaviour.

C. ligniperdus is active mainly in the evening and at night (KRZYSZTOFIAK, unpublished data), while *F. exsecta* which in interspecific communities belongs to the dominant group (PISARSKI 1973, 1982b, PISARSKI, VEPSÄLÄINEN 1981, VEPSÄLÄINEN, PISARSKI 1982) and with which *C. ligniperdus* coexists on the islands of the Tvärminne Archipelago is a typical diurnal species (PISARSKI 1982a) (Fig. 1).

INTERSPECIFIC COMPETITION

Most of the observations in this aspect were carried out in Finland, on the island Joskär. It is an inshore, rocky islet of 9 ha inhabited by 19 ant species. *C. ligniperdus* is a fairly common species there. An enormous amount of experi-

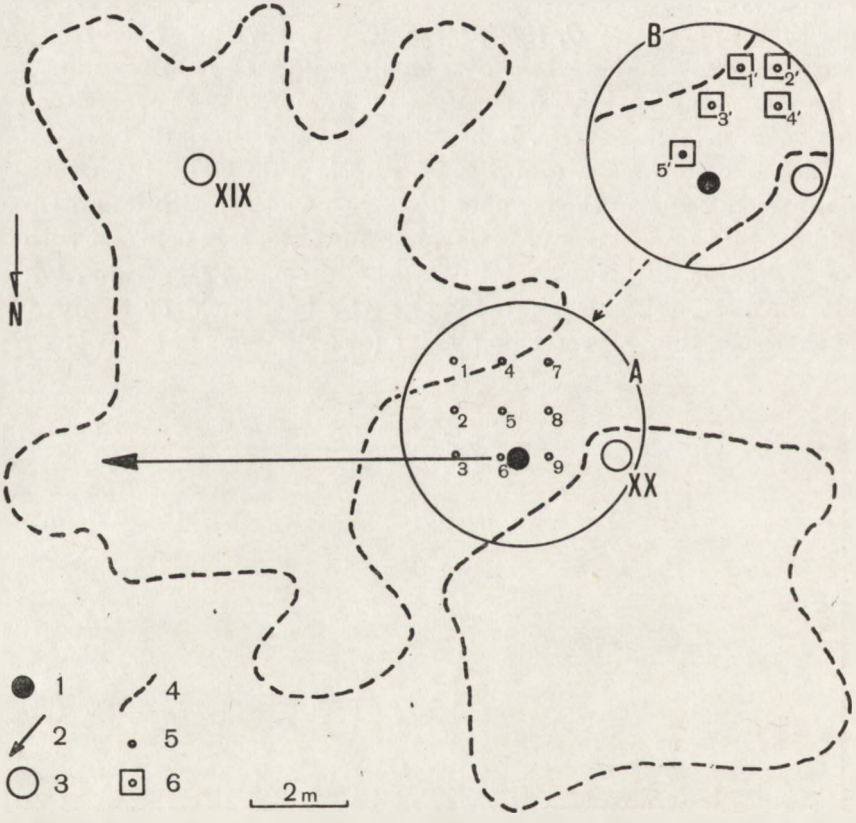

Fig. 2. Distribution of the baits in relation to the nest of *C. ligniperdus* and the nests of *F. exsecta* on the island Joskär: A — situation of the baits on 14 July 1983; B — on 17 and 18 July 1983 (1 — nest of *C. ligniperdus*; 2 — usual route of *C. ligniperdus* foragers; 3 — nest of *F. exsecta*; 4 — range of the usual penetration of the colony of *F. exsecta*; 5 — bait; 6 — bait in the biocoenometric frame).

ments with artificial food sources was carried out on the island. Baits, usually consisting of molasses, were put in many places and ants of various species were attracted to them. Alas, *C. ligniperdus* foragers apreciated the bait with moderation. They gathered in greater numbers only at the baits placed very close to their nest. At the farther ones, separate individuals stopped only transiently and there was no recruitment. Therefore, the publishable data have been taken from a series of experiments carried out on 14, 17 and 18 July 1983 in the immediate vicinity of one colony of the species under discussion. The nest of *C. ligniperdus* found in a rock crevice was situated between two large (about 0.5 m in diameter) nests of *Formica exsecta*. During some other studies they had been marked with the numbers XIX and XX and these symbols were kept (Figs 2, 3). The area was also penetrated by the following ants: *Formica fusca*, *Myrmica schencki* Em., *M. lobicornis*, *Leptothorax acervorum*, and *Leptothorax* sp. [probably *L. tuberum* (Fabr.) or *L. muscorum* (Nyl.)]. *C. ligniperdus* workers met all of them at the baits.

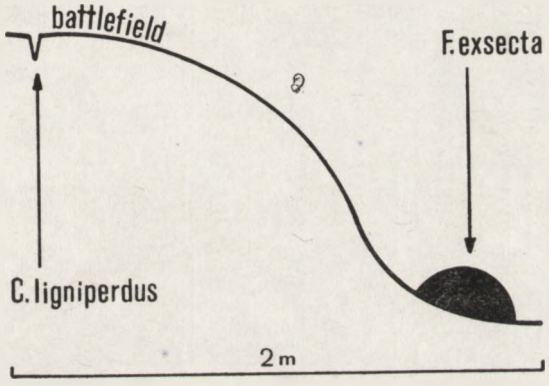

Fig. 3. Situation of the nest of *C. ligniperdus* and the nest XX of *F. exsecta* on the island Joskär.

The nest of *C. ligniperdus* was surrounded by a stretch of bare rock, which extremely facilitated the observations. The baits were in the form of blots of syrup smeared directly on the rock. Intentionally they were to be 5 cm in diameter, but they frequently spread wider. Inspections were carried out very often, even every 10–15 minutes (Tabs 1–3). Recorded were not only the ants gathered just then at the bait and eating but also individuals moving nearby, interested in the bait but probably discouraged by the presence of their competitors. Therefore, during the last two experiments the baits were placed in the centre of wire biocoenometric frames with the sides 0.5 m long. On July 14, 9 baits were placed in a regular pattern (numbers 1–9), on July 17, 5 baits (numbers 1′–5′), and on July 18, 4 of the baits placed on the previous day were refilled (1′–4′) (Fig. 2).

Table 1. Number of ants of different species at the baits on the island Joskăr, 14 July 1983 (beginning of the experiment: 9.30 a.m.)

Hour	Bait numeration	Ants at the bait						Ants in the bait vicinity
		C. ligniperdus	*F. exsecta*	*F. fusca*	*M. schencki*	*L. acervorum*	*Leptothorax* sp.	
1	2	3	4	5	6	7	8	9
9.45 a.m.	1.	—	—	—	3	—	—	
	2.	—	—	—	—	—	—	
	3.	—	—	4	—	—	—	
	4.	—	—	—	—	—	1	
	5.	1	—	1	—	3	1	no ants
	6.	2	—	—	—	—	—	
	7.	—	—	—	1	—	—	
	8.	—	—	—	—	—	—	
	9.	—	—	—	—	—	—	
10.00 a.m.	1.	—	—	—	~ 100	—	—	1 *F. exsecta*, 1 *F. fusca*
	2.	—	—	1	—	—	1	
	3.	—	—	—	—	—	—	
	4.	1	—	1	—	—	—	no ants
	5.	1	—	—	—	—	—	
	6.	5	—	—	—	—	—	2 *F. fusca*
	7.	—	—	—	4	—	—	
	8.	—	—	—	—	—	—	no ants
	9.	—	1	1	—	—	—	
10.30 a.m.	1.	—	—	—	~ 100	—	—	2 *F. fusca*
	2.	—	—	1	—	—	—	
	3.	1	—	5	—	—	—	
	4.	—	—	—	—	1	—	no ants
	5.	—	—	1	—	4	—	
	6.	19	—	—	—	—	—	2 *F. fusca*
	7.	—	—	—	8	—	—	
	8.	—	—	—	1	1	—	no ants
	9.	—	3	—	—	—	—	
11.00 a.m.	1.	—	—	—	~ 100	—	—	1 *F. exsecta*, 3 *F. fusca*
	2.	—	—	4	—	—	—	
	3.	—	—	16	—	—	—	
	4.	—	1	—	—	—	—	
	5.	—	—	5	—	—	—	
	6.	10	—	—	—	—	—	no ants
	7.	—	—	—	10	—	—	
	8.	—	—	1	—	—	—	
	9.	—	5	—	—	—	—	

Tab. 1 contd

1	2	3	4	5	6	7	8	9
1.00 p.m.	1.	—	6	—	—	—	—	14 *F. exsecta*, 15 *F. fusca*
	2.	—	5	1	—	—	—	5 *F. exsecta*, 4 *F. fusca*
	3.	no syrup						5 *F. fusca*
	4.	—	2	1	—	—	—	4 *F. exsecta*, 5 *F. fusca*
	5.	—	2	2	—	—	—	5 *F. exsecta*, 5 *F. fusca*, 3 *L. acervorum*
	6.	2	—	1	—	—	—	6 *C. ligniperdus*, 4 *F. fusca*
	7.	no syrup						6 *F. exsecta*, 4 *F. fusca*, 5 *M. schencki*
	8.	1	—	5	—	—	—	no ants
	9.	—	15	—	—	—	—	1 *F. fusca*
2.00—3.00 p.m. (general data only)	1.	*F. exsecta*						*F. fusca*, *L. acervorum*
	2.	*F. exsecta*						
	3.	*F. exsecta* (the bait restored)						
	4.	*F. exsecta*						
	5.	*F. exsecta*						
	6.	*C. ligniperdus*						
	7.	*F. exsecta* (the bait restored)						
	8.	*F. exsecta*						
	9.	*F. exsecta*						

In each case, *C. ligniperdus* foragers gathered in great numbers (up to several dozen individuals) only at the bait closest to their nest. On 14 July, it was the bait with the number 6 (40 cm from the nest), on 17 July — bait No 5′ (80 cm) and on 18 July — bait No. 3′ (160 cm). More distant baits were reached only by separate individuals, regardless of the length of the experiment. Moreover, the direction of the exploration by *C. ligniperdus* foragers was determined by the closely situated colony XX of *F. exsecta*. They exploited baits placed far from that nest and even in an area normally never penetrated by *F. exsecta* from both colonies (Fig. 2, Tabs 1–3). This did not indicate any territorialism of *C. ligniperdus* because the natural route of workers of this species going out to forage one by one led through the foraging area of colony XIX of *F. exsecta*, though it was far from the nest (Fig. 2).

During all the experiments discussed, *C. ligniperdus* and *F. exsecta* ants used the baits almost without any conflict, regardless of the numbers of each competitor. On July 14, only few *F. exsecta* workers reached the baits. At the end of the observations, baits 1–5, 7 and 8 were taken over from several to over a dozen individuals at each) by *F. exsecta* from colony XIX, bait 9 by *F. exsecta* from colony XX and bait 6 by *C. ligniperdus*. The competitors did not meet (Tab. 1, Fig. 2).

On July 17, *F. exsecta* workers from both colonies met. A battle ensued and it lasted for many hours (the conflict will be described in another paper) while the numbers of individuals at particular baits increased rapidly. The intraspecific conflict of *F. exsecta* was spread only over the area of baits 1′–4′.

Table 2. Number of ants of different species at the baits on the island Joskär, 17 July 1983 (beginning of the experiment: 8.00 a.m.)

Hour	Bait numeration	Ants at the bait							Ants in the frame						
		C. ligniperdus	*F. exsecta*	*F. fusca*	*M. schencki*	*M. lobicornis*	*L. acervorum*	*Leptothorax* sp.	*C. ligniperdus*	*F. exsecta*	*F. fusca*	*M. schencki*	*M. lobicornis*	*L. acervorum*	*Leptothorax* sp.
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
8.10 a.m.	1′.	—	—	4	—	—	—	—	—	—	1	1	—	—	—
	2′.	—	—	1	7	—	—	—	—	—	—	1	—	—	—
	3′.	—	—	2	2	—	—	—	—	—	1	—	—	—	—
	4′.	—	—	7	—	—	—	—	—	—	—	—	—	—	—
	5′.	—	—	5	3	—	—	—	—	—	—	—	—	—	—
8.20 a.m.	1′.	—	—	6	1	—	—	—	—	—	—	—	—	—	—
	2′.	—	—	1	5	—	—	—	—	—	—	—	—	—	—
	3′.	—	—	2	5	—	—	—	—	—	—	3	—	—	—
	4′.	—	—	6	—	—	—	—	—	—	1	—	—	—	—
	5′.	1	—	6	—	—	3	—	—	—	2	—	—	—	—
8.30 a.m.	1′.	—	—	9	2	—	2	—	—	—	—	3	—	1	—
	2′.	—	—	—	16	—	—	—	—	—	1	8	—	—	—
	3′.	—	—	3	17	—	2	—	—	—	1	—	—	—	—
	4′.	—	—	2	—	—	—	—	—	—	—	—	—	—	—
	5′.	—	—	7	—	—	4	—	—	—	—	—	—	—	—
8.40 a.m.	1′.	—	—	9	2	—	—	—	—	—	2	2	—	—	—
	2′.	—	—	1	35	—	—	—	—	—	—	4	—	—	—
	3′.	1	—	2	31	—	2	—	1	—	—	4	—	—	—
	4′.	—	—	1	—	—	—	—	—	—	—	—	—	—	—
	5′.	—	—	6	—	—	5	—	1	—	—	—	1	—	—
8.50 a.m.	1′.	—	—	14	9	—	1	—	—	—	—	2	—	—	—
	2′.	—	—	2	33	—	—	—	—	—	1	7	—	—	—
	3′.	—	—	2	32	—	1	—	1	—	—	—	—	1	—
	4′.	—	—	2	—	—	—	—	—	—	1	—	—	—	—
	5′.	3	—	14	—	—	2	—	1	—	2	—	—	—	—
9.50 a.m.	1′.	—	—	13	19	—	1	—	—	1	5	1	—	1	—
	2′.	—	—	2	11	—	—	—	—	—	3	13	—	—	—
	3′.	—	—	8	21	—	2	—	1	—	4	4	—	—	—
	4′.	—	—	6	—	—	—	—	—	—	2	—	—	—	—
	5′.	50	—	60	—	3	—	—	1	—	3	—	—	5	—
10.00 a.m.	1′.	1	—	4	27	—	1	—	—	—	4	3	—	—	—
	2′.	—	—	1	14	—	—	—	1	—	3	5	—	—	—
	3′.	—	—	—	25	—	—	—	—	4	14	2	—	1	—
	4′.	—	—	8	—	—	—	—	—	—	1	—	—	—	—
	5′.	27	—	23	—	—	—	—	1	—	10	—	3	1	—

Tab. 2 contd

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
10.15 a.m.	1′.	1	—	4	18	—	1	—	1	—	3	4	—	—	—
	2′.	—	—	4	13	—	—	—	—	—	7	3	—	2	—
	3′.	—	—	14	17	—	—	—	—	—	1	4	—	2	—
	4′.	—	—	10	—	—	—	—	—	—	2	—	—	—	—
	5′.	38	—	36	—	1	—	—	2	—	12	—	—	—	—
10.30 a.m.	1′.	—	—	4	16	—	—	—	1	2	3	4	—	2	—
	2′.	—	—	3	3	—	—	—	—	—	6	2	—	—	—
	3′.	—	—	7	7	—	1	—	1	1	5	—	—	2	—
	4′.	—	—	9	—	—	—	—	—	1	1	—	—	—	—
	5′.	38	—	31	—	1	—	—	4	—	8	—	—	—	—
10.45 a.m.	1′.	—	9	—	11	—	—	—	1	—	10	2	—	2	—
	2′.	1	—	4	3	—	—	—	—	—	5	3	—	—	—
	3′.	—	—	16	4	—	1	—	—	—	7	4	—	—	—
	4′.	—	1	11	—	—	—	—	—	—	5	—	—	—	—
	5′.	32	—	11	—	—	—	—	2	—	20	—	1	—	—
11.00 a.m.	1′.	—	—	10	4	—	—	—	—	—	8	2	—	1	—
	2′.	—	—	4	2	—	—	—	—	—	10	4	—	2	—
	3′.	—	—	10	2	—	—	—	—	—	10	2	—	—	—
	4′.	1	2	10	—	—	—	—	—	—	5	—	—	—	—
	5′.	33	—	2	—	—	—	—	1	—	20	—	—	—	—
11.15 a.m.	1′.	—	—	3	2	—	—	—	1	—	6	2	—	—	—
	2′.	—	—	4	1	—	—	—	—	—	9	1	—	—	—
	3′.	—	1	10	1	—	—	—	—	—	3	—	—	—	—
	4′.	—	—	6	—	—	—	—	—	1	5	—	—	—	—
	5′.	26	—	2	—	—	—	—	4	—	15	—	—	—	—
11.30 a.m.	1′.	—	—	8	3	—	—	—	—	—	6	2	—	—	—
	2′.	—	—	3	8	—	—	—	1	—	7	2	—	—	—
	3′.	—	—	15	—	—	—	—	—	—	17	—	—	1	—
	4′.	—	3	3	—	—	—	—	—	1	10	—	—	—	—
	5′.	14	—	2	—	—	—	—	4	—	10	—	1	—	—
11.45 a.m.	1′.	—	—	10	—	—	1	—	—	—	10	—	—	—	—
	2′.	—	1	1	1	2	—	—	—	—	10	1	—	—	—
	3′.	—	—	16	—	1	—	—	—	—	12	—	—	—	—
	4′.	—	1	10	1	—	—	—	—	—	15	—	—	—	—
	5′.	10	—	3	—	—	—	—	2	—	10	—	1	—	1
12.45 p.m.	1′.	—	6	2	—	—	—	—	—	2	10	—	—	—	—
	2′.	—	1	4	—	—	—	—	—	2	12	—	—	—	—
	3′.	—	—	20	—	—	—	—	—	—	15	—	—	—	1
	4′.	—	12	—	—	—	—	—	—	6	4	—	—	—	—
	5′.	7	—	3	—	—	—	—	5	—	10	—	—	—	—
1.00 p.m.	1′.	—	11	1	—	—	—	—	—	10	12	—	—	—	—
	2′.	—	3	2	—	—	—	—	—	—	15	—	—	—	—
	3′.	—	—	16	—	—	—	—	—	1	10	—	—	—	—
	4′.	—	35	—	—	—	—	—	—	7	7	—	—	—	—
	5′.	5	—	6	—	—	—	—	1	—	13	—	—	—	—

Tab. 2 contd

1	2	3	4	5	6	7	8	9	10	1	12	13	14	15	16
1.15 p.m.	1′.	—	22	—	—	—	—	—	—	3	10	—	—	—	—
	2′.	—	23	—	—	—	—	—	—	3	10	—	—	—	—
	3′.	—	—	10	—	—	—	—	1	—	12	—	—	1	—
	4′.	—	25	—	—	—	—	—	—	15	10	—	—	—	—
	5′.	11	—	3	—	—	—	—	3	—	5	—	—	—	1
1.30 p.m.	1′.	—	36	—	—	—	—	—	—	8	6	—	—	—	—
	2′.	—	23	—	—	—	—	—	—	4	8	—	—	—	—
	3′.	1	—	15	—	—	—	—	1	1	20	—	—	—	—
	4′.	—	30	—	—	—	—	—	—	8	3	—	—	—	—
	5′.	6	—	—	—	—	—	—	1	—	6	—	—	—	1
1.45 p.m.	1′.	—	45	—	—	—	—	—	—	10	8	—	—	—	—
	2′.	—	25	—	—	—	—	—	—	10	10	—	—	—	—
	3′.	2	—	16	—	—	—	—	—	4	10	—	—	—	—
	4′.	—	20	—	—	—	—	—	—	8	6	—	—	—	—
	5′.	3	—	4	—	—	—	—	2	—	10	—	—	—	—
2.00 p.m.	1′.	—	60	—	—	—	—	—	—	15	7	—	—	—	—
	2′.	—	25	—	—	—	—	—	—	5	6	—	—	—	—
	3′.	1	—	17	—	—	—	—	1	—	20	—	—	1	—
	4′.	—	25	—	—	—	—	—	—	12	5	—	—	—	—
	5′.	10	—	7	—	—	—	—	1	—	15	—	—	—	—
2.15 p.m.	1′.	—	70	—	—	—	—	—	—	15	—	—	—	—	—
	2′.	—	25	—	—	—	—	—	—	10	—	—	—	—	—
	3′.	—	1	10	—	—	—	—	1	—	—	—	—	—	—
	4′.	—	30	—	—	—	—	—	—	20	—	—	—	—	—
	5′.	3	—	4	—	—	—	—	1	—	—	—	—	1	—
2.30 p.m.	1′.	—	70	—	—	—	—	—	—	15	—	—	—	—	—
	2′.	—	15	—	—	—	—	—	—	10	—	—	—	—	—
	3′.	—	20	5	—	—	—	—	1	5	—	—	—	—	—
	4′.	—	30	—	—	—	—	—	—	10	—	—	—	—	—
	5′.	11	—	1	—	—	—	—	5	—	—	—	—	—	2
2.45 p.m.	1′.	—	70	—	—	—	—	—	1	10	2	—	—	—	—
	2′.	—	35	—	—	—	—	—	—	20	6	—	—	—	—
	3′.	—	10	2	—	—	—	—	—	5	12	—	—	1	—
	4′.	—	45	—	—	—	—	—	—	20	—	—	—	—	—
	5′.	6	—	3	—	—	—	—	1	—	10	—	—	—	—
3.00 p.m.	1′.	—	60	—	—	—	—	—	—	30	1	—	—	—	—
	2′.	—	35	—	—	—	—	—	—	30	5	—	—	—	—
	3′.	—	8	8	—	—	—	—	1	3	10	—	—	—	—
	4′.	—	30	—	—	—	—	—	—	10	—	—	—	—	—
	5′.	7	—	5	—	—	—	—	3	—	10	—	—	—	—
3.15 p.m.	1′.	—	50	—	—	—	—	—	—	35	2	—	—	—	—
	2′.	—	30	—	—	—	—	—	—	20	—	—	—	—	—
	3′.	—	16	—	—	—	—	—	1	5	15	—	—	—	—
	4′.	—	30	—	—	—	—	—	—	20	1	—	—	—	—
	5′.	4	—	3	—	—	—	—	4	—	8	—	—	—	—

Tab. 2 contd

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
3.30 p.m.	1′.	—	50	—	—	—	—	—	—	15	—	—	—	—	—
	2′.	—	20	—	—	—	—	—	—	40	1	—	—	—	—
	3′.	—	15	2	—	—	—	—	—	3	10	—	—	—	—
	4′.	—	30	—	—	—	—	—	—	25	1	—	—	—	—
	5′.	6	—	—	—	—	—	—	1	—	15	—	—	—	—
3.45 p.m.	1′.	—	35	—	—	—	—	—	—	10	2	—	—	—	—
	2′.	alarm in *F. exsecta*!							—	200	—	—	—	—	—
	3′.	—	20	—	—	—	—	—	—	10	10	—	—	—	—
	4′.	—	30	—	—	—	—	—	—	30	—	—	—	—	—
	5′.	8	—	1	—	—	—	—	5	—	10	—	—	—	2
4.00 p.m.	1′.	—	7	—	—	—	—	—	—	50	—	—	—	—	—
	2′.	alarm in *F. exsecta*!							—	150	—	—	—	—	—
	3′.	—	10	2	—	—	—	—	—	7	—	—	—	—	—
	4′.	—	40	—	—	—	—	—	—	30	—	—	—	—	—
	5′.	12	—	10	—	—	—	—	3	—	—	—	—	—	—
4.15 p.m.	1′.	—	150	—	—	—	—	—	—	20	—	—	—	—	—
	2′.	—	60	—	—	—	—	—	—	30	—	—	—	—	—
	3′.	—	10	—	—	—	—	—	—	—	7	—	—	—	—
	4′.	—	35	—	—	—	—	—	—	20	—	—	—	—	—
	5′.	15	—	1	—	—	—	—	6	—	7	—	—	—	1
4.30 p.m.	1′.	—	80	—	—	—	—	—	—	10	2	—	—	—	—
	2′.	—	40	—	—	—	—	—	—	20	—	—	—	—	—
	3′.	—	30	2	—	—	—	—	—	2	6	—	—	—	—
	4′.	—	60	—	—	—	—	—	—	20	—	—	—	—	—
	5′.	10	—	1	—	—	—	—	6	—	3	—	—	—	—
4.45 p.m.	1′.	—	80	—	—	—	—	—	—	20	—	—	—	—	—
	2′.	—	60	—	—	—	—	—	—	30	—	—	—	—	—
	3′.	—	30	—	—	—	—	—	—	10	2	—	—	—	—
	4′.	—	70	—	—	—	—	—	—	40	—	—	—	—	—
	5′.	7	—	—	—	—	—	—	4	—	15	—	—	—	—
5.00 p.m.	1′.	—	30	—	—	—	—	—	—	20	1	1	—	—	—
	2′.	—	20	—	—	—	—	—	—	25	—	—	—	—	—
	3′.	—	35	—	—	—	—	—	—	10	2	—	—	1	—
	4′.	—	50	—	—	—	—	—	—	40	—	—	—	—	—
	5′.	7	—	1	—	—	—	—	3	—	10	—	—	—	—
5.15 p.m.	1′.	—	40	—	—	—	—	—	—	20	1	—	—	—	—
	2′.	—	6	—	—	—	—	—	—	30	2	—	—	—	—
	3′.	—	30	—	—	—	—	—	—	15	6	—	—	—	—
	4′.	—	30	—	—	—	—	—	—	35	—	—	—	—	—
	5′.	5	—	5	—	—	—	—	1	—	15	—	—	—	—
5.30 p.m.	1′.	—	30	—	—	—	—	—	—	20	—	—	—	—	—
	2′.	—	—	—	—	—	—	—	—	20	1	—	—	—	—
	3′.	—	30	—	—	—	—	—	—	10	5	—	—	—	—
	4′.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	5′.	no data							no data						

Tab. 2 contd

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
6.20 p.m.	1′.	–	–	–	–	–	–	–	–	40	–	–	–	–	–
	2′.	–	–	–	–	–	–	–	–	3	–	–	–	–	–
	3′.	–	12	–	–	–	–	–	–	10	3	2	–	–	–
	4′.	–	–	–	–	–	–	–	–	5	–	–	–	–	–
	5′.	3	–	2	–	1	–	1	2	–	3	–	–	–	1

Throughout the above combat, at bait 5′ *C. ligniperdus* ants were practically undisturbed in their exploitation of the food (Tab. 2, Fig. 2).

An interesting situation developed on July 18 when, with bait 5′ missing, bait 3′ came to be the closest to the nest of *C. ligniperdus* and on the previous day the bait had been taken into possession by *F. exsecta* from colony XIX. Now *C. ligniperdus* managed to occupy it before the first *F. exsecta* scouts reached it, and it remained keeping their property until the supply of syrup was exhausted. However, the competition between these two species was not as passive as before. One hour after the bait had been put out and when it was being used by about 30 *C. ligniperdus* workers, the first *F. exsecta* individuals from colony XIX began to approach it. Then, at a distance of about 30 cm from the bait, a *C. ligniperdus* soldier (a worker of the major type) took its position between the bait and the approaching competitors. Moving within a radius of a dozen centimetres it caught approaching *F. exsecta* ants and with a snap of the mandibles crushed their heads. This never took more than a second. With its unfailing and purposeful activities the individual gave the impression of a specialized killer. After destroying a victim, it lost all interest in it. *F. exsecta* workers never fought. Upon meeting the "sentry" the either turned back in panic or (more frequently) died without any chance of defence. That situation lasted for half an hour until *F. exsecta* ants stopped coming towards the controversial bait. During that time, the *C. ligniperdus* soldier killed at least 10 *F. exsecta* individuals and one *F. fusca* ("by mistake"?). Even though its activity proved to be extremely effective this can hardly be assumed to have been the direct deterrent for *F. exsecta*. More likely, colony XIX stopped sending out foragers in that direction because there was no return information about that source of food. On the same day there was another intraspecific war of *F. exsecta* near the baits, with the exception of bait 3′ occupied by *C. ligniperdus* until the very end (Tab. 3, Fig. 2).

The behaviour of *C. ligniperdus* ants towards individual *F. exsecta* workers varied. For instance, on 17 July, at 3.15 p.m. a *C. ligniperdus* worker of the media type found near bait 3′ (within the frame; Tab. 2) drove away *F. fusca* ants it met there. However, on coming across a *F. exsecta* worker it ran away immediately. Similar cases were recorded several times, though it also happened that during such a meeting the *F. exsecta* worker was killed. It is therefore evident that aggression or submission of *C. ligniperdus* towards *F. exsecta* (in

Table 3. Number of ants of different species at the baits on the island Joskär, 18 July 1983 (beginning of the experiment: 9.15 a.m.; only *C. ligniperdus*, *F. exsecta* and *F. fusca* ants were recorded)

Hour	Bait numeration	Ants at the bait			Ants in the frame		
		C. ligniperdus	*F. exsecta*	*F. fusca*	*C. ligniperdus*	*F. exsecta*	*F. fusca*
9.30 a.m.	1′.	–	1	4	–	2	3
	2′.	–	5	1	–	4	1
	3′.	3	–	2	–	–	2
	4′.	–	50	–	–	5	–
9.45 a.m.	1′.	–	30	1	–	6	3
	2′.	–	7	2	–	3	3
	3′.	18	1	3	–	–	3
	4′.	–	100	–	–	20	–
10.00 a.m.	1′.	–	40	1	–	10	2
	2′.	–	10	1	–	10	5
	3′.	25	–	3	1	1	10
	4′.	–	100	–	–	30	–
10.15 a.m.	1′.	–	50	–	–	20	3
	2′.	–	40	–	–	20	1
	3′.	27	–	–	3	4	7
	4′.	–	40	–	–	50	–
10.30 a.m.	1′.	–	60	–	–	30	2
	2′.	–	60	–	–	30	–
	3′.	26	–	–	3	–	10
	4′.	–	20	–	–	30	–
10.45 a.m.	1′.	–	80	–	–	15	4
	2′.	–	60	–	–	40	–
	3′.	9	–	2	7	–	3
	4′.	no syrup			–	30	–

Hour	Bait numeration	Ants at the bait			Ants in the frame		
		C. ligniperdus	*F. exsecta*	*F. fusca*	*C. ligniperdus*	*F. exsecta*	*F. fusca*
11.00 a.m.	1′.	–	40	–	–	30	–
	2′.	–	30	–	–	60	–
	3′.	9	–	4	2	–	3
11.15 a.m.	1′.	–	70	–	–	20	–
	2′.	–	50	–	–	20	–
	3′.	7	–	1	2	–	3
12.00	1′.	–	70	–	–	20	2
	2′.	–	20	–	–	30	1
	3′.	2	–	1	4	–	5
12.30	1′.	–	50	–	–	10	–
	2′.	–	20	–	–	30	–
	3′.	1	–	5	3	–	5
12.45	1′.	–	20	–	–	20	1
	2′.	no syrup			–	10	1
	3′.	–	–	–	–	1	2
2.00 p.m.	1′.	–	18	–	–	15	1
	3′.	–	–	–	–	–	–
2.15 p.mp	1′.	–	15	1	–	15	2
	3′.	–	–	10	5	–	15
2.30 p.m.	1′.	–	15	1	–	10	3
	3′.	–	–	10	4	–	10
3.00 p.m.	1′.	–	–	–	–	20	7
	3′.	–	–	5	–	–	–
3.30 p.m.	1′.	–	–	–	–	20	2
	3′.	–	–	5	6	–	10

cases of incidental, individual contacts) depended on the circumstances or predisposition of a given individual.

F. exsecta is a territorial species (Pisarski 1973, 1982b) representing a group of ants situated at the top of the interspecific hierarchy (Pisarski 1980, Pisarski, Vepsäläinen 1981, 1984). The interdependences between *C. ligni-*

perdus and *F. fusca* — a typically opportunistic species — were different. *F. fusca* ants occurred commonly at all the baits, accompanying *C. ligniperdus* (and *F. exsecta*) foragers regardless of the number of their stronger rivals, apparently without any limits (Tabs 1–3).

However, a detailed analysis of the results revealed that the presence of *C. ligniperdus* at the source of food discouraged, to some extent, *F. fusca*. On the basis of the total data from July 17 and 18 it was demonstrated that in the case of baits with no *C. ligniperdus* (and *F. exsecta*) the ratio of the number of *F. fusca* foragers eating to those moving around the bait (within the frame) was higher than in the case of baits occupied by *C. ligniperdus* (even if it was only one individual). In the former case the ratio was 58%:42%, in the latter — 46%:54% (in mean numbers of individuals: 6:4 and 7:8 respectively) (Tabs 2, 3).

There was no dependence of the reaction of *F. fusca* on the number of *C. ligniperdus* individuals at the bait. Only their presence or absence was important. Moreover, the behaviour of *C. ligniperdus* workers towards *F. fusca* depended neither on their own abundance nor on the abundance of their competitors. *F. fusca* foragers were usually tolerated at the "common table". Only from time to time some *C. ligniperdus* worker frightened them with a sudden jerk of the body or rushing right into their midst, drove them away from the bait (but they immediately returned anyway). Those acts gave no impression of being decidedly aggressive. It did not seem to be the intention of a *C. ligniperdus* ant to catch its opponent. It happened very rarely indeed that an ant of *F. fusca* was killed because it had not backed in time.

It was also found out that *F. fusca* foragers were depressed more by the presence of *F. exsecta* ants than by that of *C. ligniperdus*. In the case of baits taken over by *F. exsecta*, and with no *C. ligniperdus* present, the above-mentioned ratio was 20:80% (1:4) (Tabs 2, 3).

Due to lack of comparable data it was impossible to find out whether the presence of *F. fusca* had any limiting impact on *C. ligniperdus*. There were practically no situations in which *F. fusca* ants would be absent from any of the baits (Tabs 1–3).

At the baits, apart from *F. exsecta* and *F. fusca* there were numerous *M. schencki* ants but their contacts with *C. ligniperdus* were sporadic. The data collected (Tabs 1, 2) are not sufficient for stating whether this was connected with interspecific competition or if it was accidental. The status of *M. schencki* in the hierarchy is not known. It fed at the baits together with *F. fusca*, usually without clashes. It happened only from time to time that one of the foragers drove away a *F. fusca* worker which was coming too closely. Therefore it seems that *M. schencki* is dominant over *F. fusca*.

Other ants appeared at the baits only occasionally (Tabs 1, 2).

It appears that during food competition *C. ligniperdus* ants did not manifest excessive aggression towards their competitors and, in turn, they did not fall victim to aggression of the latter. The situation was different when the nest was in danger. On the island Joskār, three such incidents were recorded — all

of them involving the above mentioned colony of *C. ligniperdus* and colony XX of *F. exsecta*. The distance between the nests of these species was about 1.8 m and each of them was situated on a different rock terrace (Fig. 3).

On 17 July 1983, at 10.15 a.m. during a bait experiment, the area of the nest of *C. ligniperdus* was invaded by over a dozen *F. exsecta* workers. They were probably attracted by the unusually great (for that part of the day; Fig. 1) commotion at the nest of their neighbour. They left after 5 minutes. There were no conflicts but 3 workers of the major type came out of the nest of *C. ligniperdus*. For a few next minutes they penetrated the area round the nest, from that side where *F. exsecta* had appeared. At 10.30 *F. exsecta* scouts appeared again. Then the number of *C. ligniperdus* soldiers increased to 5–6. They patrolled the threatened area at a stretch of 40 cm, running 10 cm from their own nest hole and perpendicularly to the line joining both nests. At the same time, the aggressors gathered in a place outside where the soldiers could not reach them. At 11.15 they returned to the entrance hole. At 11.30, from the distance of 0.5 m there came a sudden attack of about 60 *F. exsecta* workers on the nest of *C. ligniperdus*. Two soldiers were captured, the others ran away into the nest. A siege followed. About 20 *F. exsecta* workers were attacking the entrance hole which was successfully defended from within by two *C. ligniperdus* soldiers. At 11.45 the aggressors stepped back from the entrance and at 12.45 they entirely withdrew from the vicinity of the nest of *C. ligniperdus*. The losses were small: 2 dead *C. ligniperdus* individuals and several dead *F. exsecta*. The result of the conflict was that the *C. ligniperdus* colony sent fewer foragers to the bait it had taken possession of (Tab. 2). However, they did not abandon their trips across the endangered area even during the contest because they used the additional entrances to the nest.

A definitely more drastic conflict took place two days later (19 July). The observation was begun at 10.00 a.m. when the combat was in full progress. The presence of dead *F. exsecta* lying around the entrance to the nest of *C. ligniperdus* suggested that also this time that species was the attacking party. All the time 50–60 *F. exsecta* workers were involved in the conflict and they maintained constant communication with their own nest and replaced one another. On the side of *C. ligniperdus* several, up to 20, individuals (mainly of the major type) took part in the combat. These, too, moved between the battlefield and their nest. The front line (during the observations) was about 80 cm from the nest of *C. ligniperdus* which indicated that their counter-attack had been successful. From time to time, after mass raids of *F. exsecta*, the distance grew temporarily shrank (50–60 cm). However, most of the time it was just positional warfare. Close forces of *F. exsecta* stood beyond the line patrolled by *C. ligniperdus* soldiers and these never ventured forth among the forces of the enemy. They were satisfied with occasional killing of separate individuals they met. At the moments of the above mentioned raids of *F. exsecta*, the soldiers withdrew towards their nest. And in turn, when the front line was sometimes patrolled by more *C. ligniperdus* ants it was *F. exsecta* that withdrew. The aggressors

managed to seize a soldier only when it was assailed by a few workers together at the same time. That was clearly the aim of *F. exsecta* ants because they attacked in groups. While a few of them (5–8) were immobilizing the victim one sat on the back of the soldier and cut its head off. For *F. exsecta* decapitation is a characteristic way of killing the opponent (Skibińska 1982) though in the case of a *C. ligniperdus* soldier it of course takes a long time.

The conflict was finished at 11.30 when *F. exsecta* withdrew entirely. Their losses were about 100 dead individuals. *C. ligniperdus* had lost 11 soldiers and a few very mutilated ones had returned to the nest during the contest. After this incident and until the end of the studies, on 27 July, there were no further conflicts (but no bait was placed in that area).

Chronologically, the first of the conflicts recorded took place (it was provoked) on 28 July 1981. In the afternoon of that day *F. exsecta* freely penetrated the area of the *C. ligniperdus* nest even at the very entrance hole. Within the entrance there were 2–3 *C. ligniperdus* individuals, but they did not come up. Since no bait experiments had been carried in that area, the behaviour of the ants may have been considered spontaneous. At 7.00 p.m. a bait (minced meat) was put 5 cm from the entrance hole of the nest of *C. ligniperdus* (on the side nearer the nest of *F. exsecta*). After several minutes there were 5 *F. exsecta* ants at the bait and *C. ligniperdus* minor workers were beginning to leave their nest but they did not move away from the entrance. When their number increased to 10, particular individuals began to undertake short and quick raids towards the bait at which 20–30 *F. exsecta* individuals had already gathered. Attacks from both parties followed.

On the side of *C. ligniperdus*, workers of all the size classes (minor, media, major) took part in the conflict. They all behaved in a similar way, threatening their opponents with sudden jerks of the body and killing any they managed to catch. However, only soldiers ventured away from the entrance. Soldiers appeared on the ground in small numbers, for a short time and occasionally. The aggressors felt real respect for them — individual workers fled and they attacked only in groups. Minor individuals were attacked more frequently and *F. exsecta* even entered into single combat with them (and was generally beaten). The conflict came to an end at about 8.00 p.m. when *F. exsecta* withdrew. The dead included 10 *F. exsecta* ants and one *C. ligniperdus*. After their victory *C. ligniperdus* workers patrolled the area thoroughly within a radius of 0.5 m from the nest. They showed no interest in the bait and this means that their action had been caused by excessive concentration of *F. exsecta* at the nest and not by their desire to take the bait over.

The participation of minor workers in the combat may have been due to the fact that at that time this particular colony was 2 years younger than during the later (previously described) conflicts. The number of soliders may have been insufficient for driving the aggressors back.

Even before the above conflict, in June 1981, from the scene of all the future

combats (Fig. 3) there were collected dead bodies of *F. exsecta* (about 200 corpses) and *C. ligniperdus* (12 corpses). It is therefore clear that occassional contests between *C. ligniperdus* and colony XX of *F. exsecta* took place even without human interference. It is worth mentioning that the overwhelming majority of ants killed each time was left on the spot. Retreating *F. exsecta* workers carried some of their own casualties and (rarely) *C. ligniperdus* workers to their nest. *C. ligniperdus* ants were never interested in any dead bodies — regardless of the species of them.

Supplementary data on the territorial relations of *C. ligniperdus* were obtained in the Gorce Mts. There, one of the potential habitats for the species was a grassy southern slope (800–900 m above sea level) strewn with flat stones. *Formica rufa* L. was the dominant of the ant community there. Within its territories there were numerous colonies of *Formica cunicularia*, *F. fusca* and *F. lemani* BONDR. (!), *Lasius niger*, *L. flavus*, *Tetramorium caespitum*, *Manica rubida* (LATR.), *Myrmica rugulosa* NYL., *M. scabrinodis* NYL., *M. lobicornis* and *Leptothorax* sp. Under loose stones frequently were found *C. ligniperdus* queens, sometimes with larvae or even with small groups of workers. However, there were no permanent colonies of this species — with one exception. That colony, of medium size, belonged to an unusual myrmecological system. It was situated on a stony linear monticule along a road. Within an area of about 30 cm² there were 36 nests of 12 ant species — all of those mentioned above.

There was a foraging route of *F. rufa* at the edge of the system and these ants penetrated the entire area extensively. (Fig. 4). No interspecific conflicts were

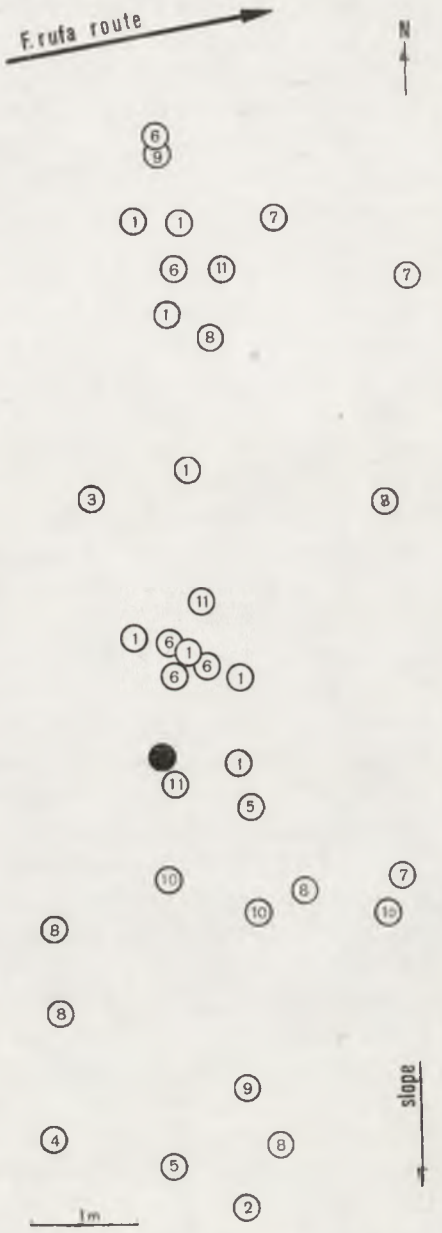

Fig. 4. Location plan of the system of the ant colonies in the Gorce Mts: ● — *C. ligniperdus*; 1 — *M. rubida*; 2 — *M. rugulosa*; 3 — *M. scabrinodis*; 4 — *M. lobicornis*; 5 — *Leptothorax* sp.; 6 — *T. caespitum*; 7 — *L. niger*; 8 — *L. flavus*; 9 — *F. fusca*; 10 — *F. lemani*; 11 — *F. cunicularia*.

recorded. *C. ligniperdus* ants left their nest separately and, undisturbed, crossed the territory of the system of foreign colonies going to their foraging area situated beyond that area. The only direction they avoided was that towards the route of *F. rufa*.

INTRASPECIFIC COMPETITION

On 19 July 1985, a battlefield of *C. ligniperdus* was found in the Gorce Mts. It stretched partly on the edge and partly on the slope of a narrow gorge with spruces at its borders. The trees grew every few metres, and almost in each of them there was a nest of *C. ligniperdus*. Between two spruces 4.5 m apart the ground was littered with dead ants of the species under discussion. Some of the dead bodies were old and withered but most of them were quite fresh; even here and there a limb twitched. Since nothing unusual had been recorded there on the previous day, the battle must have taken place during the night. The greatest amount of fresh dead bodies was found along a two-metres-shaped line which must have been the front line (Fig. 5).

The battlefield was first inspected at about 5.00 p.m. On both sides of the line of dead bodies there were several dozen scattered and wounded individuals (soldiers). Some stayed motionless in one place, others milled around. Separate healthy workers went to and from along the line joining the nests. On encountering another ant, these two felt each other with their antennae and parted without any visible signs of hostility. They never paid the least attention to the dead and wounded individuals.

At 6.00 p.m., a single combat between two soldiers started. It was very peculiar and nothing in it resembled the fierce battles of other ant species. It turned out however, that it was not a ritualized combat. It was fought almost in one place. First, for half an hour, the ants stood facing each other and repeatedly flexing their abdomens. They obviously tried to snatch the other's mandibles. Their raised fore legs were constantly in motion, thus giving an impression as if the ants were pushing the other away. All their movements were very slow. At one moment, one soldier managed to snap its mandibles on a leg of its opponent and very nearly bit it off, but that had no effect on the pace of the combat. The action suddenly accelerated when one ant got hold the abdomen of the other. Up till then, other workers moving past had paid no attention to the fighters. Now 3 soldiers stopped near them. At first, it was difficult to decide whether they belonged to the same colony or to different ones. Their behaviour towards each other and towards the fighting ants was not explicit, yet they displayed no apparent hostility. After a few moments of milling around and feeling the fighters with their antennae they joined in the combat separately and casually, catching one of the opponents with their mandibles. Seconds later that ant had its abdomen and all the legs cut off. The "assistants" went away leaving the "victor" — with two legs missing and the body of its opponent stick-

Fig. 5. Region of the *C. ligniperdus* intraspecific combat in the Gorce Mts. (short markers – the front line; long markers – spruces with the nests) (Photo T. Płodowski).

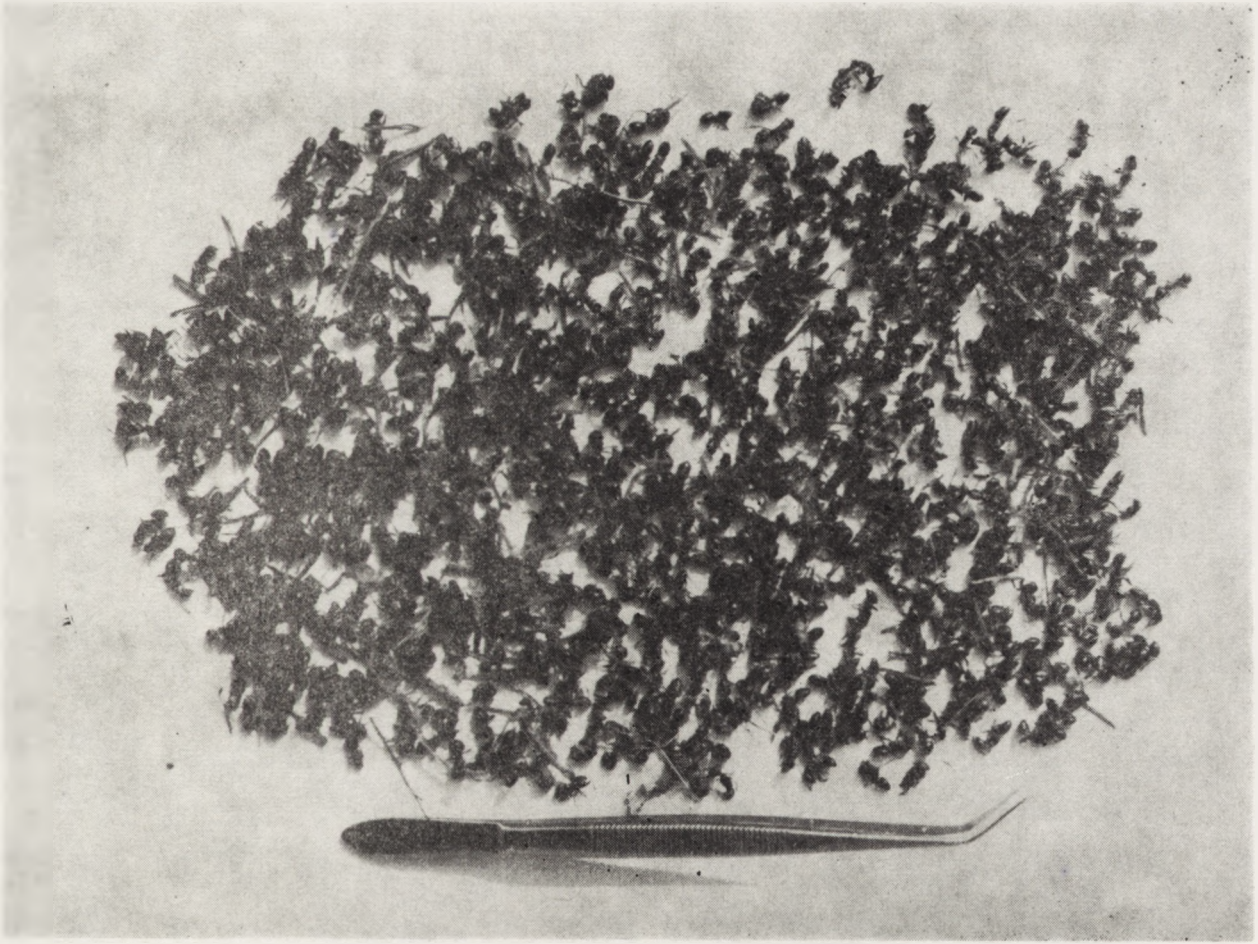

Fig. 6. Total of *C. ligniperdus* dead bodies collected from the battlefield in the Gorce Mts. on 19 July 1985 (Photo T. Płodowski).

ing to its antennae — milling around helplessly. A dubious success after a seventy--minute fight.

An analysis of the wounds of ants collected from the battle field indicates that all combats were carried out in a similar way. Over 600 dead ants were found there (Fig. 6); most of them were workers of the major type. With a clasp of the mandibles, 70 dead bodies were firmly joined into pairs: in 12 pairs the

Fig. 7. Typical bodily injuries of *C. ligniperdus* individuals as a result of intraspecific combat in the Gorce Mts. (Photo T. Płodowski).

individuals had caught each other by the mandibles, in 12 — by the antenna, in 10 — by a leg, in one — by the abdomen. Usually, one of the corpses was wounded markedly (legs, antennae, abdomen or head cut off). The other was intact (or almost intact) — it had probably died after the combat, as a result of venom poisoning (Fig. 7).

After the above massacre, peace reigned for a few days. On 23 July, about 100 new fresh corpses of *C. ligniperdus* were found in the same place. After that, until the end of the season, nothing happened there even though the former front line was constantly crossed by individuals from both colonies.[1]

DISCUSSION

In the light of the data presented, the position of *C. ligniperdus* in the interspecific structure of ant communities seems to be clear. It is a nonterritorial species (not defending the borders and territory of its foraging area) which defends its food sources and the nest. According to the theory of the three--level hierarchical structure of ant communities (Pisarski 1973, 1980, Reznikova 1980, 1982, Czechowski 1982, Vepsäläinen, Pisarski 1982, Pisarski, Vepsäläinen 1981, 1984) this places the species within the second (middle) group. Of course, this theory is only a rough, schematic representation of the real situation. It is gradually being improved by accumulated knowledge about inter- and intraspecific relations among ants. It is, however, far from being final due to the variety of potential situations, enriched further by the behavioural plasticity of ants.

The life strategy and war tactics of *C. ligniperdus* are puzzling. Lack of expansiveness in this species was revealed even in their use of baits. As opposed to many species with a strong tendency to constantly take over and exploit new food sources, *C. ligniperdus* ants basically used only those baits which were within the safe zone near the nest. These they defended actively (and successfully) against a species higher up in the interspecific hierarchy. This moderation of *C. ligniperdus* was also clearly manifested during their conflicts with *F. exsecta*. All the combats recorded were definitely defensive. Only very few individuals were engaged in them — just the smallest number sufficient for repulsing the aggressors. This economy in utilizing the potential of the colony was especially distinct in the actions of soldiers operating in insignificant numbers and clearly adapted to individual actions. (The very conspicuous lack of help for individuals in danger probably resulted from the fact that there was no proper signalling between individuals). It is evident that in contacts with *F. exsecta C. ligniperdus* assumes the position of a subordinate species. Some amount of aggressiveness towards the dominant is contained within the strategy of the "lowest risk". Sporadic acts of aggression towards the colony of *C. ligniperdus* may be seen as a mechanism forcing the potentially dangerous rivals for food to give up their penetration of at least a part of the territory of the dominant. It has been demonstrated that even just a single *C. ligniperdus* individual can make it impossible for *F. exsecta* to use a source of food by interrupting the flow of information between that source and the nest.

[1] In early July 1986, an identical conflict occurred there. Then, to the end of the season, a peaceful co-existence of the two colonies was observed. In 1987, there were no contests between the *C. ligniperdus* swarms at that place [W.Cz.].

Most probably, a significant role in the mutual relations between *C. ligniperdus* and *F. exsecta* is played by the difference in circadian rhytms in activity of these ants. It may be assumed that this "time lag" enables *C. ligniperdus* to nest very close to the colonies of the dominant species. Bearing in mind the time of the observations, the behaviour of *C. ligniperdus* foragers at the baits may have been limited to some extent by the time of day inopportune for them. In cases of conflicts with *F. exsecta* such a possibility is rather out of the question (Fig. 1). Anyway, the problem of interspecific relations of *C. ligniperdus* and other ants in the aspect of time requires an unmistakable explanation.

The recorded phenomena of interspecific relations of *C. ligniperdus* were fairly easy to interpret. Unfortunately, the same cannot be said about the above mentioned case of intraspecific behaviour. There is nothing unusual in the fact that two communities of the same species fight. Nonterritorial species may have no natural mechanism which would make it possible for alien communities to coexist with them fairly peacefully. *C. ligniperdus* is a nonterritorial species in intraspecific relations, this being manifested by the fact that individuals from both colonies mixed also when the combat was over. Odd is the cause of a conflict and its result — a massacre on both sides. Intraspecific wars (even those of territorial species) resulting in tremendous losses on both sides, occur in times of scarcity of food, especially of protein. Then, the dead bodies are carefully picked up and used as food in the nest. Such cannibalistic predation is well known in species of the *Formica rufa* group: *F. rufa* (Le Moli et al. 1982), *F. polyctena* (de Bruyn, Mabelis 1972, Mabelis 1979a, b, 1984a, b), and *F. lugubris* Zett. (Breen 1977, Le Moli, Parmigiani 1982, Cherix 1983). However, in the case under discussion the dead ants were left on the battlefield. So the combat between the colonies of *C. ligniperdus* had not been caused by food shortage.

The number of casualties was striking. To lose several hundred workers of the major subcaste in one instance must have been a grave loss to the colony of *C. ligniperdus*. It is all the more incomprehensible in view of the economical war tactics of these species employed in their contacts with *F. exsecta*. If not directly aimed at obtaining food, intraspecific combats of many ants are incomparably less fierce. They are either ritualized, as in *Myrmecocystus mimicus* Wheeler (Hölldobler 1976, 1979, Hölldobler, Lumsden 1980) and *Lasius niger* (Czechowski 1984a) or, even if they seem extremely fierce there are few casualties as in *Tetramorium caespitum* (McCook 1872, Weber 1965) and *Myrmica laevinodis* (Stawarski 1961, Czechowski 1984b).

However, it is also a well-known fact that the degree of aggression between foreign ants of the same species is varied. It covers a wide range from merely touching each other with the antennae to a deadly fight. There is a hypothesis about certain factors inhibiting aggression that may appear insufficient under special circumstances (situation of a colony, frequency of encounters with alien individuals). This gives rise to contradictory information on intraspecific relations, for instance in the case of species from the genus *Pogonomyrmex* Mayr

(De Vita 1979). It so happened that two colonies of *P. occidentalis* (Cresson) peacefully used the same foraging route for a long time and then, suddenly, one day they began to fight (Clark, Comanor 1973).

According to the idea of De Vita (1975), intraspecific aggressiveness may be conditioned by the proportion of the abundance of neighbouring colonies. The more even their forces, the more probable are competitive encounters that cause accumulation of mutual hostility. It is not unlikely that that was the reason for the intraspecific conflict of *C. ligniperdus*. The explosion of aggression may have been enhanced by the high, even abundance of both colonies and by their being situated very closely (too closely?). It is quite probable that the whole area occupied by *C. ligniperdus* was overpopulated by these ants.

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STRESZCZENIE

[Tytuł: Międzygatunkowe i wewnątrzgatunkowe stosunki konkurencyjne u *Camponotus ligniperdus* (Latr.) (*Hymenoptera, Formicidae*)]

Przedmiotem pracy są zachowania konkurencyjne robotnic *Camponotus ligniperdus* (Latr.) wobec innych mrówek (i vice versa), zwłaszcza *Formica exsecta* Nyl. i *F. fusca* L., a także wobec obcych przedstawicieli własnego ga-

tunku. Rozważany jest status *C. ligniperdus* w międzygatunkowej organizacji zespołów *Formicidae*. Badania (eksperymenty i obserwacje spontanicznych zachowań mrówek) przeprowadzono w latach 1981 i 1983 na wyspie Joskär Archipelagu Tvärminne (południowa Finlandia) oraz w r. 1985 w Gorcach (południowa Polska).

Na podstawie uzyskanych danych *C. ligniperdus* określono jako gatunek nieterytorialny, broniący źródeł pokarmu i (oczywiście) gniazda. W myśl teorii 3-stopniowej hierarchicznej struktury zespołów mrówek, zapewnia mu to przynależność do drugiej (pośredniej) grupy gatunków.

W kontaktach z gatunkiem hierarchicznie dominującym (*F. exsecta*), mrówki *C. ligniperdus* przejawiają strategię życiową „najmniejszego ryzyka". Z oferowanych im sztucznych źródeł pokarmu (karmniki z syropem) wykorzystują tylko najbliższe gniazdu. W sytuacjach konfliktowych przyjmują postawę obronną, angażując do walki minimalną liczbę osobników, jaka jest niezbędna do odparcia agresji. Dysponując ogromną siłą fizyczną, mrówki *C. ligniperdus* (typu major) są potencjalnie bardzo groźne. Agresywność przejawiają jednak rzadko, zmuszone okolicznościami. Niekiedy (wobec braku innego pożywienia) mogą się nawet stawać wyspecjalizowanymi myrmekofagami, a ich łupem padają mrówki wyżej usytuowane w hierarchii (*Formica polyctena* Foerst.).

Wobec gatunków hierarchicznie podporządkowanych (*F. fusca*) zachowują się obojętnie lub co najwyżej przejawiają agresywność pozorowaną. Sama jednak obecność robotnic *C. ligniperdus* przy źródle pokarmu wpływa w pewnym stopniu odstraszająco na tę grupę konkurentów.

W relacjach wewnątrzgatunkowych *C. ligniperdus* zdarzają się konflikty między sąsiadującymi ze sobą społeczeństwami. Walki, prawdopodobnie spowodowane przegęszczeniem populacji, są wyniszczające dla obu stron. Warunkują jednak późniejszą, już bezkonfliktową, koegzystencję na wspólnie wykorzystywanym obszarze.

РЕЗЮМЕ

[Заглавие: Межвидовая и внутривидовая конкуренция у *Camponotus ligniperdus* (Latr.) (*Hymenoptera, Formicidae*)]

Предметом обработки является изучение конкурентного поведения рабочих муравьев у *Camponotus ligniperdus* (Latr.) по отношению к другим муравьям (и наоборот), особенно *Formica exsecta* Nyl. и *F. fusca* L., а также чужим представителям собственного вида. Обсуждается статус *C. ligniperdus* в межвидовой организации сообществ *Formicidae*. Исследования (эксперименты и наблюдения спонтанного поведения муравьев) были проведены в 1981 и в 1983 годах на острове Йоскер (архипелаг Тверминне в южной Финляндии) и в 1985 году в Горцах (южная Польша).

На основании полученных данных *C. ligniperdus* определен как вид нетеррито-

риальный, защищающий источники пищи и (конечно) гнезда. Согласно 3-степенной иерархии структуры сообществ муравьев этот вид можно причислить ко второй (промежуточной) группе видов.

При встрече с видом доминирующим в иерархии (*F. exsecta*) муравьи *C. ligniperdus* проявляют жизненную стратегию „наименьшего риска". Из предложенных им искусственных источников пищи (кормушки с сиропом) используют только те, которые находятся ближе всего к гнезду. В случае конфликта принимают оборонительную позицию, используя для борьбы минимальное количество особей, необходимое для отражения агрессии. Обладая огромной физической силой, муравьи *C. ligniperdus* (типа *major*) могли бы быть грозными. Но их агрессивность проявляется редко и в вынужденных ситуациях. Иногда (в связи с отсутствием иной пищи) они могут стать специализированными мырмекофагами, а их жертвами становятся муравьи находящиеся на более высокой ступени иерархии (*Formica polyctena* Foerst.).

По отношению к нижестоящим в иерархии (*F. fusca*) они проявляют безразличие или в крайнем случае мнимую агрессивность. Однако, уже само присутствие у источников пищи рабочих *C. ligniperdus* действует в какой-то степени отпугивающим образом на эту группу конкурентов.

Во внутривидовых отношениях *C. ligniperdus* случаются коифликты между живущими по соседству сообществами. Борьба между ними вызывается, по-видимому, чрезмерной плотность популяции и является губительной для обеих сторон. Однако, она обуславливает дальнейшее бесконфликтное сосуществование на совместно используемом участке.

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