POLISH ACADEMY OF SCIENCES ★ INSTITUTE OF ZOOLOGY
MEMORABILIA ZOOLOGICA

MEMORABILIA ZOOL.	44	83–91	1990

Wojciech CZECHOWSKI

Aggression of *Formica aquilonia* YARR. to *Camponotus ligniperdus* (LATR.) (*Hymenoptera, Formicidae*) under the conditions of artificial colonization

Abstract. A conflict between an artificially founded colony of *Formica aquilonia* YARR. and a native colony of *Camponotus ligniperdus* (LATR.) is described. The observations were carried out in the Tvärminne archipelago (southern Finland) in 1987. The phenomenon has been discussed in the context of the specificity of the species biology and the theory of the hierarchic organization of ant communities.

INTRODUCTION

In 1987, on islands of the Tvärminne archipelago (Tvärminne Zoological Station, the Helsinki University) in southern Finland there were conducted experiments on artificial colonization of red wood ants under extreme habitat conditions. The experiments were connected with colonization studies going on under mountain conditions in Poland (PISARSKI, CZECHOWSKI 1990a,b. The ants colonized on the islands, while fitting in with the structure of the local communities, clashed with the native ants. The most spectacular conflict was one between the artificially introduced *Formica aquilonia* YARR. and the local *Camponotus ligniperdus* (LATR.) on the island of Vikaskär. *F. aquilonia*, the red wood ant, a territorial species, belongs to the highest, dominant group in the three-level competition hierarchy of interspecific ant communities (PISARSKI 1980, VEPSÄLÄINEN, PISARSKI 1982, PISARSKI, VEPSÄLÄINEN 1989). The hierarchic status of *C. ligniperdus* as a species of the intermediate group (non-territorial, defending its sources of food) has been defined in a recent paper (CZECHOWSKI, PISARSKI 1988). The present one supplements that previous work.

DESCRIPTION OF THE OBSERVATION

The Tvärminne archipelago is formed by typical granite skerries with cliff shores. Due to enormous topographic variety of the islands, all the succession stages – from the bare rock to the climax formation – are concentrated over a small area. The climax formation there is a pine forest with features of the taiga (SAVOLAINEN, VEPSÄLÄINEN 1988) (Fig. 1). The variety of plant communities is reflected in a varied character of ant assemblages; the myrmecofauna is rich both in the qualitative and the quantitative respects (VEPSÄLÄINEN, PISARSKI 1982).

The size of the island of Vikaskär is about 2 ha and most of its surface is overgrown with the forest. During the studies the natural myrmecofauna consisted of

Formica lugubris ZETT. and *F. exsecta* NYL. (territorial species, dominant in the hierarchy), *Lasius niger* (L.), *L. flavus* (FABR.) and *Camponotus ligniperdus* (non-territorial species, defending their sources of food), and *Formica fusca* L., *Myrmica laevinodis* NYL. and *Leptothorax* spp. (non-territorial, opportunistic species).

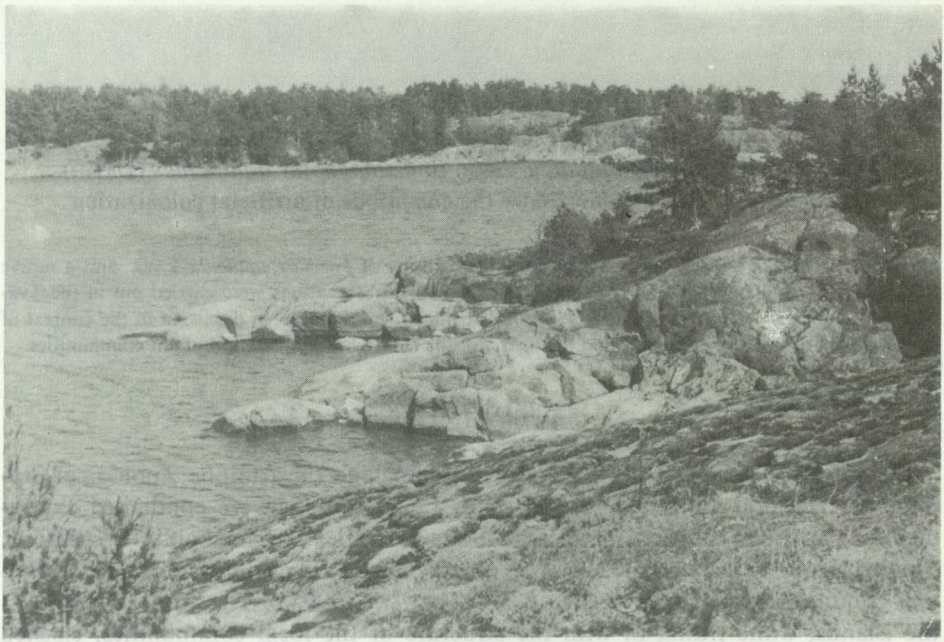

Fig. 1. Landscape of the Tvärminne archipelago (in the foreground – the northern coast of Vikaskär, in the background – Joskär) (Photo by W. CZECHOWSKI).

In June, two *F. aquilonia* colonies and one of *F. polyctena* FOERST. were artificially settled on Vikaskär. All of them had come from large nests on the mainland. The colonization was carried out along the general principles that quarantee the proper functioning of newly-founded colonies (PISARSKI, CZECHOWSKI 1990b,) (Fig. 2).

Colony V-aq-II of *F. aquilonia* was founded on 20 June, after taking about 100 dec^3 of material from the maternal nest ($\varnothing = 1.7$ m, $h = 0.5$ m). The new nest was situated on the eastern edge of the forest that was sparse just there (Fig. 3). After three days the "artificial" colony was supplied with a large batch of workers from the maternal nest. After a week the mound of the new nest had a diameter of 1 m and a height of 30 cm. (Some flattening of the artificially made mound during the first days after foundation is caused by workers searching for buried pupae. When the "rescue operation" is over, ants undertake a rapid enlargement of their nest or move to a new place). The abundance of Colony V-aq-II was judged to be 250–300 thousand workers.

Towards the south, facing the forest, the colony of *F. aquilonia* was next to a group of nests of hierarchically subordinate species. Within a radius of 15 m there were recorded 12 colonies of *F. fusca*, 5 of *L. flavus*, 3 of *M. laevinodis*, and 1 of *C. ligniperdus*. The main foraging route of *F. fusca* and *C. ligniperdus* (used by both

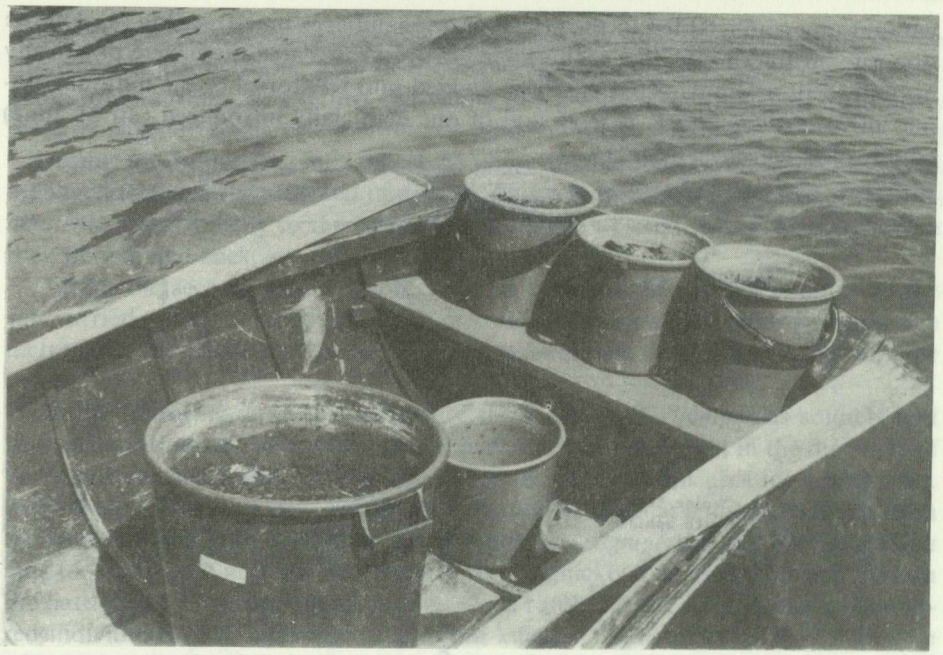

Fig. 2. Material for the artificial colonization of red wood ants prepared for transport under the conditions of the Tvärminne archipelago (Photo by W. CZECHOWSKI).

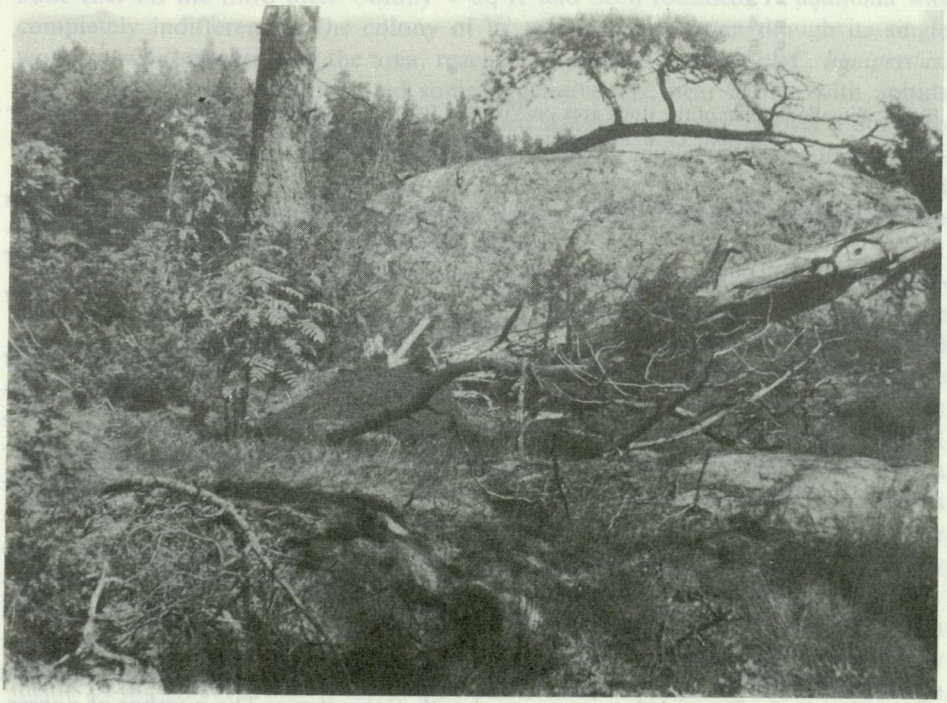

Fig. 3. Situation of the artificial colony of *F. aquilonia* on Vikaskär (Photo by W. CZECHOWSKI).

without any conflicts) led to the crown of a magnificent pine-tree (Fig. 4). On the opposite, northern side, in a rocky, sparcely overgrown area there were practically no non-territorial ants. That part was divided into territories of the natural colonies of *F. lugubris* and *F. exsecta* and of one artificially introduced (on 21 June) colony of *F. polyctena* (V-p-I).

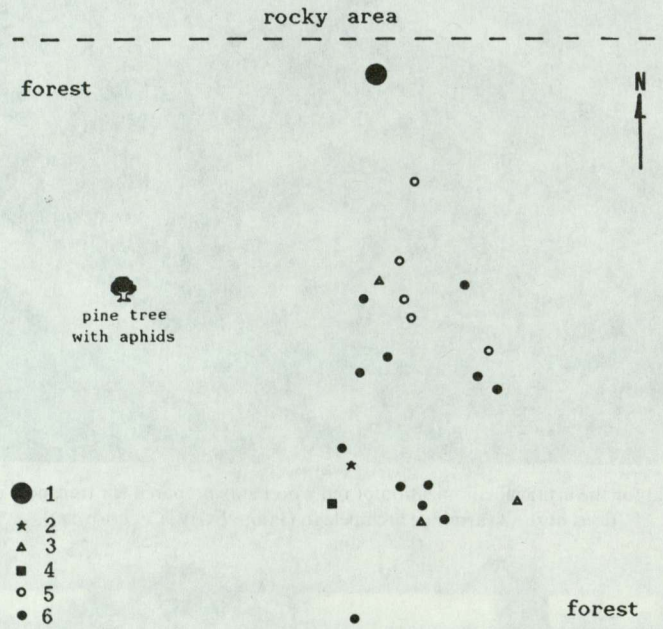

Fig. 4. Situational plan of the study area on Vikaskär (nests: 1 – "artificial" *F. aquilonia*; 2 – *C. ligniperdus*; 3 – *M. laevinodis*, 4 – *L. niger*; 5 – *L. flavus*; 6 – *F. fusca*).

Colony V-aq-II was founded at 16.00. Two hours later, numerous *F. aquilonia* workers that were penetrating the vicinity began fierce attacks on the nearby (situated within 11 m) nests of *F. fusca*. Before dusk the first scouts found the colony of *C. ligniperdus* inhabiting a dead pine that was 11 m from the nest of *F. aquilonia* (Fig. 4). The nest entrance was in the trunk, 0.5 m above the ground.

Next morning *F. aquilonia* attacked the nest of *C. ligniperdus*, leaving the *F. fusca* colonies alone. At 10.30, when the observations were commenced, a furious combat was going on under the tree inhabited by *C. ligniperdus*. The assault had come from one side of the base of the trunk and there the mass of defenders rallied over a belt 10 cm wide and stretching for 0.5 m in a semicircular way. In this zone the density of *C. ligniperdus* was 20–30 individuals per 1 dec^2. Farther on (20–30 cm from the trunk) they were more dispersed. A constant exchange of workers was maintained between the battlefield and the nest (along the trunk). During this phase of the combat (and later) about 200 individuals, mainly the major and medium forms, took part in the conflict on the side of *C. ligniperdus*. During the first period of observations (until 12.00) they kept controlling one zone up to 30 cm from the trunk. Beyond that it swarmed with *F. aquilonia*. The number of aggressors engaged in the conflict at one time was assumed to be several thousand *C.*

ligniperdus soldiers, fighting individually (without any signs of mutual help), on the front line killed, with one grab of the mandibles, dozens of *F. aquilonia* workers. From time to time they, in turn, fell victim to a group of fighting aggressors when these managed to pull a defender into the midst of their own forces.

During the initial (but not detected) phase of the conflict the aggressors had managed to reach the attacked nest itself. This was indicated by a heap of dead *F. aquilonia* stuck directly to the trunk (Fig. 5). Some time must have elapsed before they were forced back.

During the second period of observations (16.00–18.00) a firm counter attack was carried out by *C. ligniperdus*. Dense groups of these ants moved to almost one metre from the trunk and drove away *F. aquilonia* that were clearly retreating just then.

On the following day (22 June), since the morning, *C. ligniperdus* soldiers had been penetrating intensively the vicinity over 1 m from their nest in the direction of the attack the day before. *F. aquilonia* failed to appear in this area for a long time. Only about 14.00 did a new, relatively mild conflict begin at a distance of 2 m from the trunk inhabited by *C. ligniperdus*. About 30 *C. ligniperdus* and 50 *F. aquilonia* ants took part in it at first. The latter, however, quickly increased their numbers on the battlefield. Their opponents did not. As a result of this, at 18.00, several hundred individuals of *F. aquilonia* caught and killed *C. ligniperdus* soldiers that were still penetrating the area separately.

That was the end of the severe phase of the conflict between the colonies. On 23 June (i.e. on the third after Colony V-aq-II had been founded) *F. aquilonia* was completely indifferent to the colony of its recent enemy, even though its single workers, while penetrating the area, reached far beyond the nest of *C. ligniperdus*. The latter, in turn, demonstrated some aggressiveness; near a pine with aphids (several metres from its nest; Fig. 4) it formed stationary groups of over a dozen to 30 individuals which murdered lonely workers of *F. aquilonia*. These groups forbade *F. aquilonia* foragers access to the main source of food in the area that had originally been exploited by *C. ligniperdus* and *F. fusca*, then temporarily taken into sole possession by the new hosts of the territory.

On the following day, however, a normal (i.e. dispersed) penetration of *C. ligniperdus* and also that of the decimated *F. fusca* population was restored over the entire area previously explored by both species. (The colonies of *F. fusca* attacked on the first day by *F. aquilonia* had not been liquidated, simply their abundance was limited). No conflicts were recorded. The trunk of the honeydew-giving pine was climbed upon, in peace, by (single) workers of *C. ligniperdus, F. fusca*, and *F. aquilonia* (!). Yet the number of the foragers of the first two species was much lower than before the introduction of *F. aquilonia*. It can be assumed, on the basis of the ethology of *C. ligniperdus* and *F. aquilonia*, that in the pine crown their foragers went two different ways (and the opportunistic *F. fusca* could, as fancy took it, exploit the supplies reserved by either species).

The conflict was a very "bloody" one. Since neither party took away their own or the enemy's casualties, it was possible to collect them from the battlefield by means of the biocoenometric method. A frame of 10 × 10 cm was used. There were 12 squares (the total area of 1200 cm^2) situated linearly and in these 2401 dead ants were found: 2362 specimens of *F. aquilonia* and 39 ones of *C. ligniperdus*. The total

number of the casualties of the conflict was a little higher: about 2500 *F. aquilonia* and about 50 *C. ligniperdus* individuals. The mean density of corpses along the line of the most fierce skirmishes (a belt of 10–20 cm extending for one metre from the base of the trunk of *C. ligniperdus* towards the nest of *F. aquilonia*) was 200/dec². At some spots (10–20 cm from the trunk) it was over 500/dec² (5 dead ants in 1 cm² !). The spatial distribution of the corpses of both species is presented in Fig. 5.

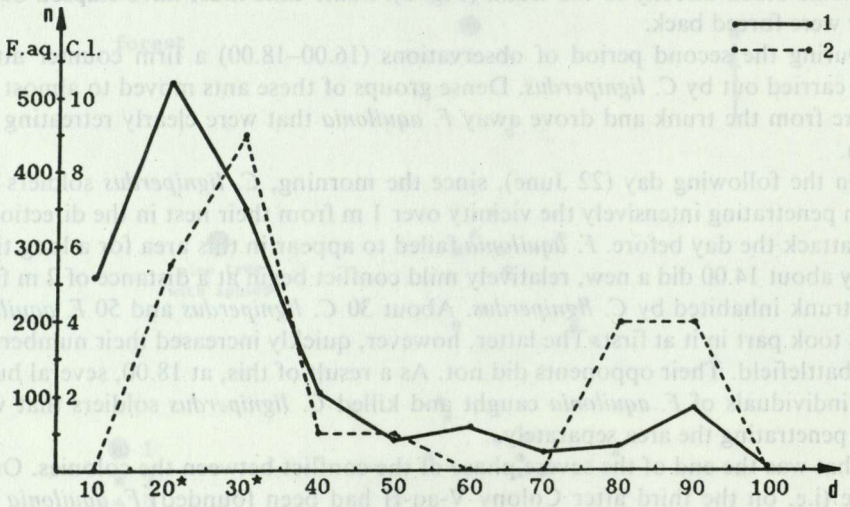

Fig. 5. Spatial distribution of the dead bodies of *F. aquilonia* (1) and *C. ligniperdus* (2) along the line of the combat [n – number of corpses of each species over 1 dec²; d – distance (in cm) from the nest of *C. ligniperdus* (* – the mean data from two squares)].

The end of the conflict between *F. aquilonia* and *C. ligniperdus* coincided with the beginning of a conflict between Colony V-aq-II and a newly founded colony of *F. polyctena* V–p–I. The distance between the "artificial" nests was 14 m in a straight line. The real distance was several metres longer because of the complicated sculpture of the earth's surface. The conflict lasted 2 days (23 and 24 June) and ended when *F. polyctena* retreated and limited the range of its penetration towards Nest V-aq-II.

DISCUSSION

The results of the experiment presented here fully confirmed what had been stated in a previous paper (CZECHOWSKI, PISARSKI 1988), namely the hierarchic position of *C. ligniperdus* as a non-territorial species that defends its nest and sources of food. The competition strategy and the war tactics of this species that had been hinted upon in the quoted paper were much more evident in the present investigation. *C. ligniperdus*, ants with great physical strenght, behave in a strikingly reserved way during aggressive contacts with hierarchically higher competitors. Their alarm recruitment is very slow and they become really involved in the conflict only at the critical moment, when their nest is directly threatened. Even any likely offen-

sive actions (in order to get back some lost sources of food) are conducted with moderation. Soldiers, even if they happen to be in groups, fight separately, and do not pay attention when an individual is threatened. This means that they do not expose one another during a conflict with a collectively fighting enemy such as, for instance, the red wood ants.

The war tactics of *C. ligniperdus* has a distinctly adaptative sense. It makes it possible to gain, at the minimum cost, the aims dictated by the life strategy of the species.* This is best illustrated by the events described here. 98% of the casualties of the conflict were *F. aquilonia* ants. The death of one *C. ligniperdus* soldier was paid for by the lives of 60 attackers. While losing no more than 0.5% of the swarm (the colony of *C. ligniperdus* had at least over a dozen thousand individuals) the ants managed to defend their nest and to win the right to exploit (which may have been essential to their existance) the sources of food. The balance of gains and losses for *F. aquilonia* seems far less positive. The colony lost about 1% of its potential in order to restrict, at the most, the penetration of a (not very dangerous) rival to food. This, apparently, is the price for the highest position in the competition hierarchy – a position attainable only to species whose societies have 10^5–10^6 individuals (PISARSKI, VEPSÄLÄINEN 1989).

---

* It must be pointed out that such a strategy of *C. ligniperdus* applies only in interspecific contacts. During intraspecific conflicts the situation is fundamentally different (CZECHOWSKI, PISARSKI 1988).

There may arise a question why *F. aquilonia* attacked so fiercely the nests of subordinate species if, according to the theory of the hierarchic organization of interespecific ant communities, such species can nest and forage within the territory of the dominant colony (PISARSKI 1973, 1982, CZECHOWSKI 1982, PISARSKI, VEPSÄLÄINEN 1989). Doesn't this contradict the theory?

Well, the fact is that non-territorial species may nest in the foraging area of their territorial neighbour, yet not as they please, but in a definite order imposed by the owner of the territory. The colonies of territorial species play the role of centres for the spatial organization of multi-specific ant communities, as was demonstrated by SAVOLAINEN and VEPSÄLÄINEN (1988) in the Tvärminne archipelago. There must be (under given habitat conditions) a certain minimum distance between the nests of definite species. It can be supposed [W. CZ.] that this distance depends not only on the biological specificity of the partners but on the abundance (the biotic potential) of their colonies as well. If this is the case then a justification can easily be found for the aggression of the artificially introduced colony of *F. aquilonia* toward the subordinate species, bringing about a decrease in their impact on the environment.

It is worth mentioning that the aggressiveness of *F. aquilonia* was selective – victimizing only *F. fusca* and *C. ligniperdus* – apparently the most dangerous competitors in that particular situation. Nests of *Myrmica leavinodis, Lasius flavus*, and *L. niger* were situated within the range of Colony V-aq-II, yet they remained undisturbed. However, they were relatively far from the nest of *F. aquilonia* and, what is more, proportionally to their competitive position in the community: the underground *L. flavus* – 5–8 m away, the opportunistic *M. laevinodis* – 5.5–12 m, the food-defending *L. niger* – 11.5 m (Fig. 4). At the same time, a colony of *F. polyctena* (P-p-I) was established on the nearby island of Porsgrundet, and it immedia-

tely destroyed all the numerous colonies of *M. laevinodis* within a radius of 2–3 m from its nest.

The intensity of competition between different species may be inferred from the distances at which they nest. A species that may nest in the immediate vicinity of the mound of red wood ants, almost at their foot, is *Manica rubida* (LATR.) – a mountain ant that is only slightly (or not at all) inferior to red ants in respect of the size of workers. In the Gorce Mts. (southern Poland) it commonly accompanies natural colonies of *Formica rufa* L. and frequently those of *F. polyctena*. Even artificially founded colonies tolerate it, though after a temporary conflict, as a neighbour. The biology of *M. rubida* is known very poorly. There are opinions that these ants do not use any animal food. This is not true because several cases have been recorded in the Gorce Mts. when these ants, in groups, hunted invertebrates, mainly earthworms. There is no doubt, however, that they are hardly any competitors for red wood ants.

Returning to the aggressive behaviour of *F. aquilonia* from Vikaskär, two additional reasons for this may be hypothesized. Firstly, subordinate species are sometimes expelled by territorial colonies when these reach a very high density of individuals in the foraging area (PISARSKI 1982). Such a situation occurs (temporarily) during the first days after building an artificial nest. The aggressive behaviour of ants may be purely automatic then. When the density returns to normal, the reaction disappears. Secondly, ants (colonies) of different species that are neighbours and meet constantly, get used to one another so that their aggressiveness is weaker than in alien ants (colonies) (Sejma 1971). In the situation described the partners were obviously total strangers and the resulting temporary conflicts may be considered a peculiar way of getting to know one another. This sounds comical, but there has been recorded a concrete case of a severe conflict between colonies of *F. sanguinea* (one of these moved voluntarily near the nest of the other), and after this there were no hostile reactions (CZECHOWSKI 1990).

REFERENCES

CZECHOWSKI W. 1982. Stosunki konkurencyjne wśród mrówek. Wiad. entomol., Warszawa, **3**: 111–125.

CZECHOWSKI W. 1990. A raid of *Formica sanguinea* LATR. (*Hymenoptera, Formicidae*) on a conspecific colony. Memorabilia zool., Warszawa, 44: 00–00.

CZECHOWSKI W., PISARSKI B. 1988. Inter- and intraspecific relations in *Camponotus ligniperdus* (LATR.) (*Hymenoptera, Formicidae*). Ann. zool., Warszawa, **41**: 355–381.

PISARSKI B. 1973. Struktura społeczna *Formica* (*C.*) *exsecta* NYL. (*Hymenoptera: Formicidae*) i jej wpływ na morfologię, ekologię i etologię gatunku. IZ PAN, Warszawa, 134 pp.

PISARSKI B. 1980. Evolution of the competitive behaviour in social insects. Insectes soc., Paris. **27**: 284–287.

PISARSKI B. 1982. Territoires et territorialisme de *Formica* (*Coptoformica*) *exsecta* NYL. In: Structure et organisation des sociétés de fourmis de l'espèce *Formica* (*Coptoformica*) *exsecta* NYL. (*Hymenoptera, Formicidae*). Memorabilia zool., Wrocław, **38**: 163–203.

PISARSKI B., CZECHOWSKI W. 1990a. Modalites de colonisation des fourmis du grouppe *Formica rufa* au Parc National de Gorce (Pologne). Actes Coll. Insect. soc., Lausanne, **6**: 237–242.

PISARSKI B., CZECHOWSKI W. 1990b. The course of the artificial colonization of red wood ants in the Gorce National Park. Memorabilia zool., Warszawa, 44: 00–00.

PISARSKI B., VEPSÄLÄINEN K. 1989. Competition hierarchies in ant communities (*Hymenoptera, Formicidae*). Ann. zool., Warszawa, **42**: 321–329.

SAVOLAINEN R., VEPSÄLÄINEN K. 1988. A competition hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos, Copenhagen, **51**: 135–155.

SEJMA F.A. 1971. K voprosu ob otnošenijach murav'ev s ochraniaemymi territorijami. In: Murav'i i zaščita lesa. Moskva, pp. 69–71.

VEPSÄLÄINEN K., PISARSKI B., 1982. Assembly of island ant communities. Ann. zool. fenn., Helsinki, **19**: 327–335.

Instytut Zoologii PAN
ul. Wilcza 64
00-679 Warszawa (Poland)

STRESZCZENIE

Agresja *Formica aquilonia* YARR. wobec *Camponotus ligniperdus* (LATR.) (*Hymenoptera, Formicidae*) w warunkach sztucznej kolonizacji

Opisany jest konflikt między eksperymentalnie założonym mrowiskiem *Formica aquilonia* YARR. (agresorem) i naturalnym mrowiskiem *Camponotus ligniperdus* (LATR.) (stroną napadniętą). Podczas 3-dniowego konfliktu zostało zabitych ok. 3 tysięcy osobników *F. aquilonia* i ok. 50 osobników *C. ligniperdus*. Zaatakowanym mrówkom udało się obronić gniazdo i zyskać możliwość wspólnego z *F. aquilonia* eksploatowania głównego na ich polu troficznym źródła pokarmu – drzewa z mszycami. Eksperyment przeprowadzono na wyspie Vikaskär (Archipelag Tvärminne, południowa Finlandia) w 1987 r. Prześledzone zjawiska przedyskutowano w kontekście specyfiki biologii gatunków – stron konfliktu na tle teorii hierarchicznej organizacji zespołów mrówek.