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Wojciech CZECHOWSKI

Intraspecific conflict in *Formica exsecta* NYL. (*Hymenoptera, Formicidae*)

Abstract. An experimentally provoked conflict between two monocalic colonies of *Formica exsecta* NYL. is described. The observations were made in the Tvärminne archipelago (southern Finland) in 1983. The phenomenon is discussed in the context of the biology of the species and the local habitat conditions.

INTRODUCTION

Formica (*Coptoformica*) *exsecta* NYL. lives in the northern Palaearctic. It is photophilous, ecotonal species – it occurs on the edges of forests, in forest clearings, and in habitats of the early succession stages (clearings with sparse bushes, young tree stands, etc.), as well in light forests. The mounds of its nests (whose diameter usually is 20–30 cm) are constructed from small plant remnants. *F. exsecta* forms monogynic or polygynic, monocalic or polycalic societies. It is a territorial species, i.e., within the hierarchic structure of ant communities it belongs to the group of the dominants.

A monograph on the biology of *F. exsecta* is included in a study supervised by PISARSKI (1982a). The present paper is a supplement.

STUDY AREA AND A DESCRIPTION OF THE OBSERVATIONS

The observations were carried out on the island of Joskär in the Tvärminne archipelago on the Baltic Sea, off the southern coast of Finland. The island is a rocky granite skerry about 10 ha in size. It is covered with vegetation at all the succession stages – from patches of lichen and moss on the rocks, through juniper thickets and clusters of pine trees, to the climax formation which means there a pine forest with a well-developed stratum of brushwood (*Vaccinium* L., *Empetrum* L., *Calluna* SALISB., *Ledum* L. (See: Fig. 1 in: CZECHOWSKI 1990).

Within the myrmecofauna of Joskär the group of territorial species consists of *Formica polyctena* FOERST., *F. lugubris* ZETT., *F. truncorum* Fabr., and *F. exsecta*. As a result of competitive interactions these ants divided the area between themselves. *F. exsecta*, a species on the lowest position in the hierarchy (within the dominant group), was left with the poorest habitats – small patches of juniper thickets with separate stunted pine trees dispersed among bare rocks (VEPSÄLÄINEN, PISARSKI 1982, SAVOLAINEN, VEPSÄLÄINEN 1988, PISARSKI, VEPSÄLÄINEN 1989) (Fig. 1).

During the 1980's the population of *F. exsecta* on Joskär included about 40 colonies [many of them have been disregarded on the map in a paper by PISARSKI & VEPSÄLÄINEN (1989)]. The average diameter of a nest was 40 cm and its height 15 cm (according to the state in 1987; pers. data). The colonies were grouped in several centres and one of these, situated in the south-western part of the island, was studied more closely in 1983.

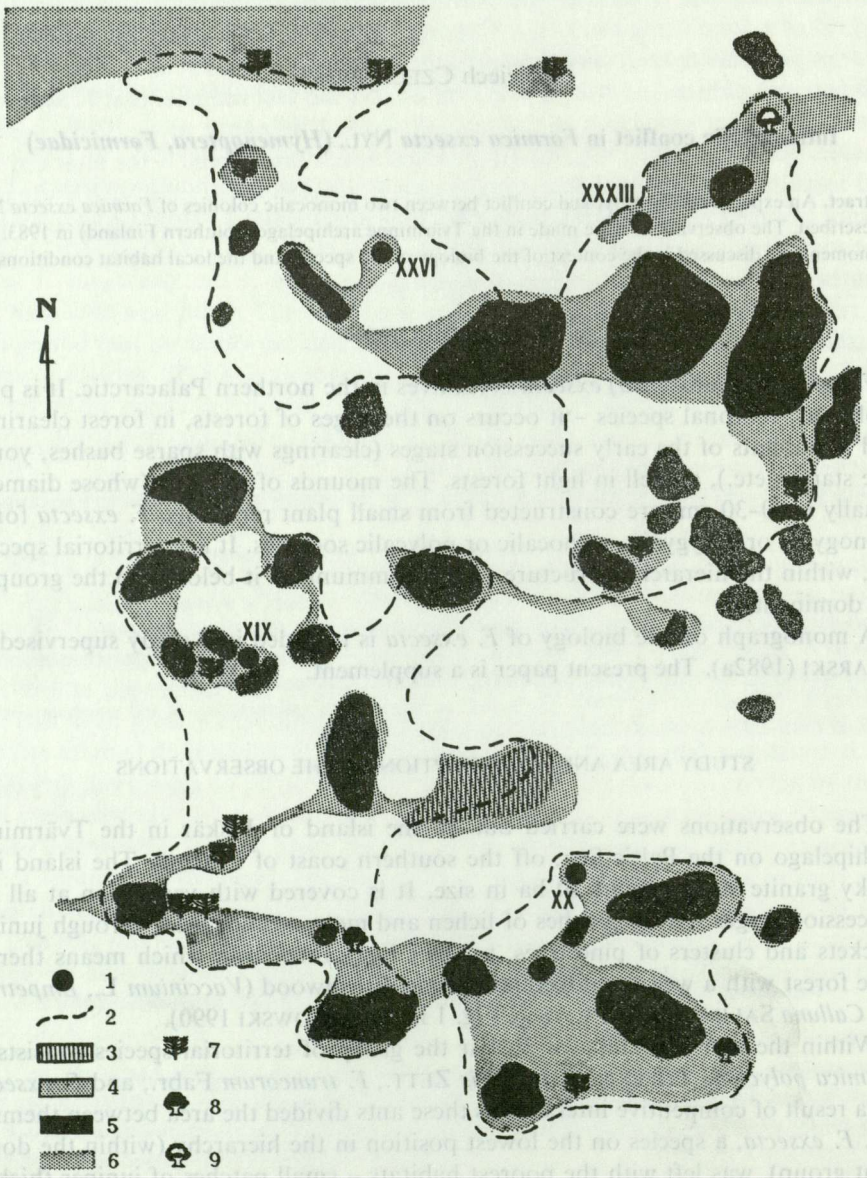

Fig. 1. Vegetation in the area of the studied group of *F. exsecta* colonies on Joskär [1 – nest; 2 – territorial border of the colony; 3 – bare rock (possibly moss and lichen); 4 – herbaceous vegetation (grass); 5 – juniper thicket; 6 – raspberries; 7 – pine tree; 8 – birch; 9 – sorb].

The group of *F. exsecta* colonies under discussion consisted, during the study, of 4 inhabited nests (XIX, XX, XXVI, XXXIII; according to the numbering by PISARSKI & VEPSÄLÄINEN). They were distributed over a mosaic area in a way characteristic of the local conditions – each in a separate patch of vegetation. The penetration ranges of particular colonies did not meet, they were separated by belts of "no ants' land" (or rather "no ants' rock") (Fig. 1). The average distance between the nests was 13 m, the average diameter of a nest reached 50 cm and the height 20 cm, and the average territory of one colony was about 60 m² (Table). All the colonies were considered "very active" and this means that, in relation to their size, the nests had a maximum number of individuals.

Table. Parameters of the studied *F. exsecta* colonies on Joskär: diameter (∅) and height (h) of the nest, size of the territory (t), and value of the index of aggressiveness (a)

Colony	∅	h	t	a
XIX	85/55 cm	20	79 m²	0%
XX	65/50 cm	30	49 m²	100%
XXVI	40/30 cm	10	50 m²	100%
XXXIII	30/25 cm	10	74 m²	0%

According to PISARSKI & VEPSÄLÄINEN (1989) the abundance of *F. exsecta* colonies on Joskär reaches 10^4 individuals. This was apparently confirmed by an attempt at determining the abundance of particular colonies by means of the LINCOLN method [markings and repeated catches of individuals; PĘTAL, PISARSKI (1981)]. The number recorded for Colony XIX was 6200 and that for Colony XX – 7000 individuals. These numbers, however, are lowered for obvious reasons because the method used wrongly assumes that the entire swarm takes part in the functions outside the nest and that ants mix evenly within their nest. The actual abundance of the colonies was undoubtedly several times higher. A test carried out by PISARSKI revealed no aggressiveness of Colony XIX and 100-per-cent aggressiveness of Colony XX (within their own nests) towards strange *F. exsecta* workers (Table).

In July 1987, this area was the scene of experiments and observations on interspecific competitive relations in *Camponotus ligniperdus* (LATR.) (CZECHOWSKI, PISARSKI 1988), and among others on relations with *F. exsecta*. The studied colony of *C. ligniperdus* nested in a rock crevice within the free zone between the territories of Colonies XIX and XX of *F. exsecta*. During the experiments an intraspecific conflict between these ants was provoked. Nests XIX and XX were situated at 10.5 m from each other. The territories of the colonies were separated by a 2–3.5 m belt. Only in one place did they come as close as 0.8 m (Figs 1, 2).

On 14 July, at 9.30, 9 baits with syrup were placed on the rock dividing the territories of Colonies XIX and XX (Fig. 2). At 10.00, Bait 9, the one closest to the border of the range of Colony XX, was found by the first forager from this colony. At 11.00, Bait 4 situated on the border of the territory of Colony XIX was discovered by the first worker from there. By 15.00 almost all the baits had been occupied

by *F. exsecta*: Baits 1–5, 7 and 9 by foragers from Colony XIX, and Bait 9 by foragers from Colony XX. (Bait 6 was used by *C. ligniperdus*).

On that day there were few *F. exsecta* foragers at the baits – at any given moment there were several, and 15 at most, individuals using one bait [for details see: CZECHOWSKI, PISARSKI (1988)]. Ants from both nests must have felt insecure in a strange area, particularly those from Colony XX. The reaction of the latter was connected with the topography of the area. Nest XX (and the territory of the colony) was situated on a terrace lower than that of Nest XIX, its territory and all the baits. In order to reach the part with baits *F. exsecta* workers from Colony XX had to climb along a vertical fault 0.5 m high.

Between 15.00 and 16.00, near Bait 6 (and this was near the nest of *C. ligniperdus*) there occurred a clash between *F. exsecta* from Colony XX and *C. ligniperdus* and later there took place the first hostile contacts between *F. exsecta* workers from Nests XIX and XX that met there just then. Intraspecific aggressiveness appeared to be stronger than interspecific. In some instances an *F. exsecta* ant attacked a conspecific enemy while it was fighting with a *C. ligniperdus* individual, and did not pay any attention to the latter.

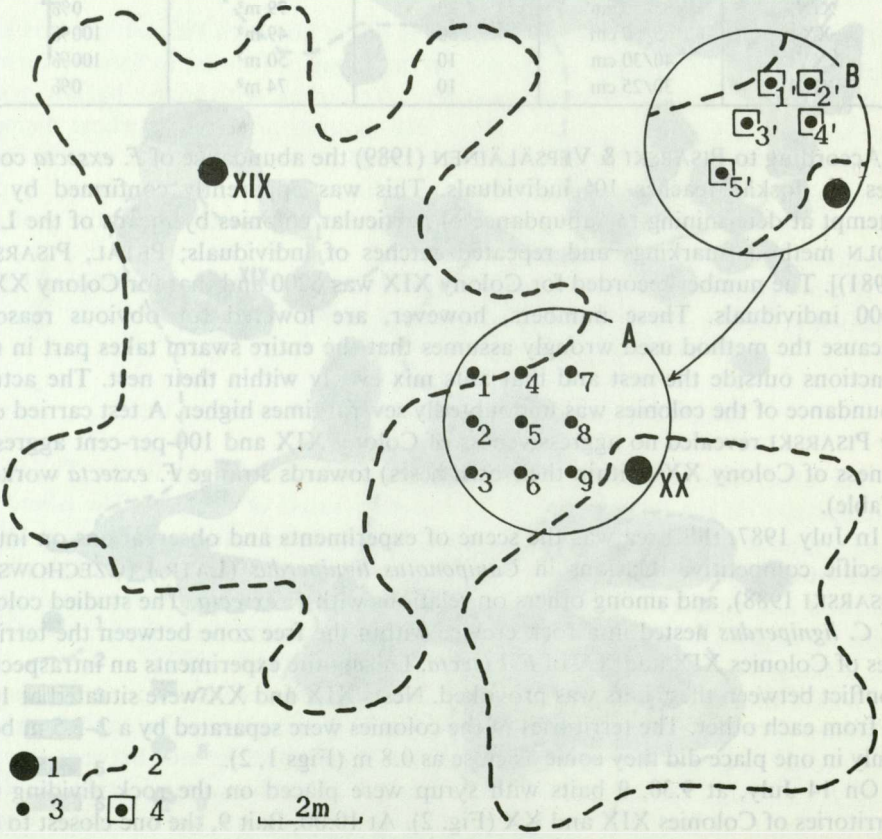

Fig. 2. Distribution of baits within the locality of Colonies XIX and XX on Joskär on 14 July (A) and 17 and 18 July 1983 (B) [1 – nest; 2 – territorial border of the colony; 3 – bait; 4 – bait within a biocoenometric frame (plot)].

The beginning of the conflicts was accompanied by a considerable increase in the abundance of *F. exsecta* in the area under discussion – the density was several individuals per 1 dec^2. Later this increased to over a dozen, and at some places to 20–30/dec^2. The individuals were mainly those from Colony XX. Ants from Colony XIX were not numerous and at dusk they retreated completely.

On the following day, i.e., 15 July (when the baits had not been refilled) the area of the conflict was intensively penetrated by *F. exsecta* from Colony XX. Ants from Nest XIX did not venture so far, and *C. ligniperdus* remained hidden in its nest. On 16 July the situation was quite normal again.

The experiment was repeated on 17 July. At 8.00, 5 baits were put out and this time each of them was placed in the middle of a biocoenometric frame, the side of which was 0.5 m (Fig. 2). Later, this made it possible to precisely determine the movements of the ants. No *F. exsecta* ant appeared near the baits before 10.45. Later, however, these ants took possession of all the baits but Bait 5′. All the time, almost from the beginning of the experiment to the end of the day, this bait was at the disposal of *C. ligniperdus* – regardless of the events happening nearby (CZECHOWSKI, PISARSKI 1988).

The first baits takes for good by numerous *F. exsecta* ants were Bait 4′ (Colony XX) and Baits 1′ and 2′ (Colony XIX). From 13.00 (4′) to 13.15 (1′, 2′) to the evening the baits were continuously utilized usually by several dozen ants at a time. Bait 3′ was taken by *F. exsecta* (XIX) 1.5 h later and as a source of food it was the least popular (see: CZECHOWSKI, PISARSKI 1988). Yet this was the very place where the first contact of hostile ants occurred on that day and near this bait a two-day conspecifis conflict was begun. It was initiated by an attack of about 30 workers from Colony XIX directed at 3 ants from Colony XX which, at 15.30, came up to the occupied bait. After 15 minutes the conflict moved to Plot (the frame) 2′. The recruitment to this plot was very strong on the part of ants from Nest XIX (about 100 individuals/0.25 m^2 along the nest-frame route) and weaker on the part of those from Nest XX (about 10 ind./0.25m^2). Within the plot (frame) there were over 200 ants involved in about a dozen skirmishes. In the course of a few minutes, the workers from Colony XX were driven away from the frame and they fled to their nest. However, about 10 of them remained at Bait 4′. Later that day only occassional clashes (single combats) were recorded between Plots 2′ and 4′ (Fig. 2).

Colony XX became very active on the following day (18 July). In the morning its workers began to intensively penetrate the upper (not their own) rocky terrace, venturing farther and farther on. At 9.00, about 40 of them were in Plot 4′, about 20 in 2′, and several in 1′. Workers from Colony XIX gathered at Plot 1′ and soon took possession of in. At 9.15, the baits in Plots 1′–4′ were refilled (there was no trace of syrup in them). Within half an hour they were taken over by *F. exsecta* (with the exception of Bait 3′ because untill 16.00 it was occupied by *C. ligniperdus*. Such a state of affairs (several dozen to a hundred ants at a bait) was maintained all the time.

For a long time the ants did not show any pronounced aggressiveness although their numbers and density in the disputed area were high. Only single individuals, if they had gone too far away from the masses of nestmates, were caught and killed by the opponent. At about 10.00, a group of 30 workers from nest XX undertook

some organized raids (feigned attacks?) going from Plot 4′ towards Plot 1′ occupied (as the only one) by Colony XIX. Each time, however, at the last moment before a conflict the wave of the attackers rapidly turned back. After this there was a period of relative peace (only separate individuals were attacked).

At midday, a group of 20 individuals from Colony XIX gathered at the borderline of their territory (on the level with Plot 1′; Fig. 2), more workers began to arrive from the nest and these were carrying dead ants or (less frequently) empty pupal cocoons (in one case it was the head of *C. ligniperdus*). They left this "luggage" on the rock, most often near the border of their territory but a few tried (successfully) to penetrate among their opponents close to Plot 2′. The same behaviour was soon recorded in ants from Colony XX. From 12.00 to 12.40, 20 such cases were observed on the part of Colony XIX and 2 cases on the part of Colony

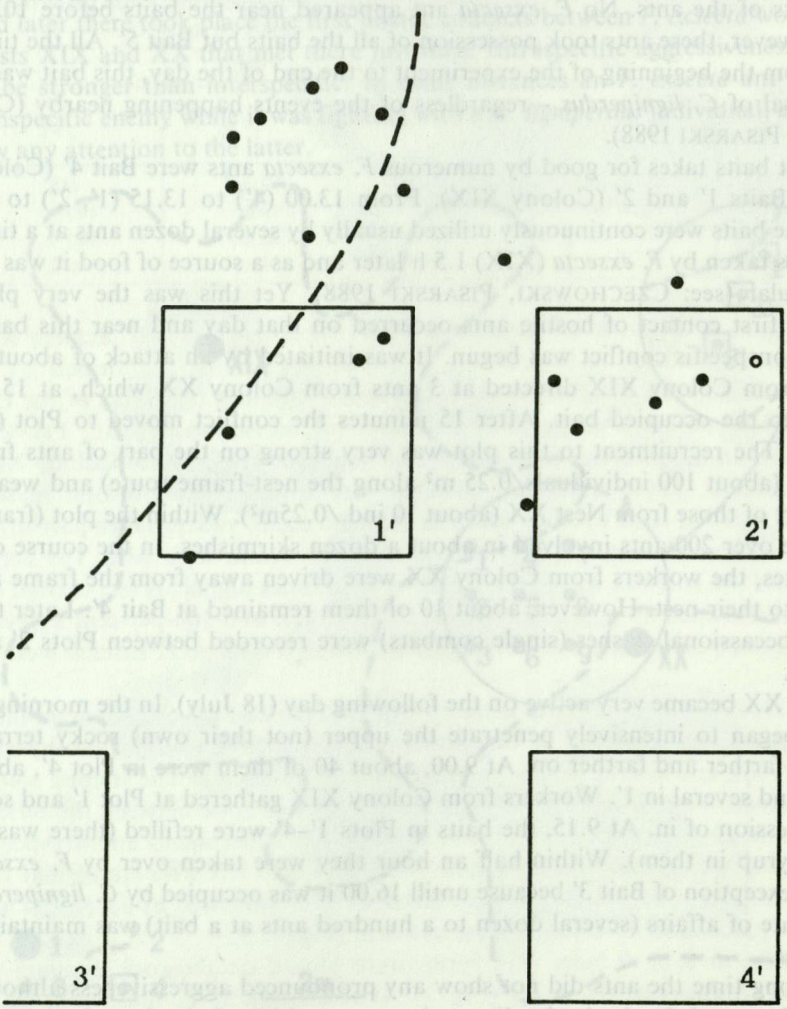

Fig. 3. Places where dead ants were left by workers from Colonies XIX (●) and XX (○) in relation to the territorial border of Colony XIX and to the biocoenometric frames (plots).

XX (Fig. 3). This phenomenon had been recorded in other ant species (but in interspecific relations) and it always preceded (foretold?) a conflict (CZECHOWSKI 1975a, 1977, 1985, 1989).

True enough. During this time the frequency of individual combats rapidly increased. The attitude of the ants visibly changed: so far they had avoided contacts, now they strove for skirmishes. At 12.45, about 50 workers from Colony XIX conducted a sudden raid from beyond their territorial border to the middle of the area occupied by the enemy (between the frames). The attacked ants immediately formed a compact group similar in number. For half an hour the organized groups fought against each other, either clashing or running away, with the attitude of the ants from Colony XX being rather defensive. The front line was moved within about 4 m^2 of the rock separating the territories. No recruitment from the nests was recorded. The battle was over after half an hour. The casualties included about 50 ants from Colony XX and about 10 from Colony XIX. The dead were taken to the nests and ants returned to the baits. As a result of the battle Colony XIX took over Bait 2′ (in addition to Bait 1′ occupied earlier) (Fig. 2).

At about 17.00, the number of ants in the disputed area began to grow again and the frequency of aggressive encounters increased. At 17.15, about 150 workers from Colony XIX suddenly invaded Plot 4′. within 15 minutes they seized the whole area, having killed over 60 enemies and lost about 10 individuals. During that time *F. exsecta* from Colony XX undertook several mass counterattacks and each time it retreated towards the nest. Recruitment from both nests was very intensive. At 17.50, the front line remained steady just on the edge of the fault above Colony XX and then waves of the attackers began to retreat through Plot 4′ to Plot 2′. Dead ants were taken away too.

At 18.10, the forces of Colony XIX attacked again, reached to the very edge of the fault of the rock – and were suddenly defeated. The defeat was brought about by two factors. In this place and on the whole vertical face there were hundreds of ants from Colony XX (their nest was directly threatened). And the topography of the area was advantageous for the defenders. The fighting ants fell off the smooth rock almost directly onto Nest XX and this naturally put the attackers in a hopeless position. They lost about 100 individuals within 5 minutes, the recruitment from Colony XIX ceased, and at 18.15 the attackers withdrew to Plot 1′. The other plots (and the baits) were almost deserted.

On that day the observations were finished at 18.30. At that time both sides sent out only single scouts – Colony XX from the bend of the rock, Colony XIX from Plot 1′. No contacts were recorded. During the following days (when there were no more experiments with baits) the situation became normal. The colonies returned to their usual ranges.

An inspection made in this area in 1987 confirmed the status quo ante.

DISCUSSION

The question of the social structure of the *F. exsecta* colonies on Joskär has not been explained. There is no direct evidence proving that they were either mono- or polygynic. The enormous mutual aggressiveness could suggest monogyny. At least

such is the behaviour of monogynic (unlike that of polygynic) colonies of *F. exsecta* in Poland (PISARSKI 1973, 1982c). However, the studies in Poland have been conducted under habitat conditions totally different from those in Finland. There seems to be a risk when the bionomic, and especially the behavioural, characteristics of one population are ascribed uncritically to another one that lives under different conditions. [E.g. *F. pressilabris* NYL., a species closely related to *F. exsecta*, can form huge polycalic colonies in the central part of its specific range (CZECHOWSKI 1975b, 1976) whereas on the range edges it occurs only in a monocalic form (DLUSSKY 1967).

Certain data testify to polygyny in *F. exsecta* on Joskär. This is indirectly indicated by the occurrence of nest aggregations in different parts of the island. It may be assumed that there are genetic relationships between the colonies within each aggregation. What is more, during many years of myrmecological studies on Joskär (VEPSÄLÄINEN & PISARSKI) it was occasionaly recorded that new *F. exsecta* colonies were formed by fissions of maternal colonies. (At the same time, however, some new colonies were founded by single queens, and these were, at least originally, monogynic ones). Of course, colony fission is possible only in polygynic society. Therefore, at least some *F. exsecta* colonies on the island are of this character. The local population, however, is morphologically fairly homogeneous although workers of this species from mono- and polygynic colonies differ perceptibly (PISARSKI 1973, PISARSKI, BANERT 1982). It may therefore be hypothesized that Colonies XIX and XX (XXVI and XXXIII too) were polygynic colonies of the same origin but, as a result of the local habitat conditions, they had lost contact with each other and become mutually hostile.

These conditions are not difficult to describe. They are in contrast to those that in Poland are favourable to the formation of permanent polycalic societies of *F. exsecta*. Such a society springs into existance as a result of colony fission when filial swarms settle near their maternal nests. In a fairly homogeneous habitat (a forest clearing, sparce young tree stand) there are many places suitable for founding a nest. In such a situation (and when food is abundant) filial nests may be founded on the egde of the territory belonging to the maternal colony or not very far from its border. Thanks to this the foraging areas of the maternal and filial colonies partly overlap or at lest they touch (PISARSKI 1973, 1982b, CHUDZICKA 1982a). Such a distribution is adventageous for permanent contacts among foragers and for intercolonial exchange of food and individuals. These very factors are of vital importance for the integration of a polycalic society (PISARSKI 1973, CHUDZICKA 1982b).

F. exsecta has no such possibilities on the Finnish rocks. As already mentioned, the stronger competitors there have driven it to habitats that are rather poor and small in size. Finding suitable places for nests is difficult in small patches of vegetation where the layer of soil is usually very thin. On Joskär (and on other islands of the archipelago) *F. exsecta* often nests in rock crevices and builds the mound directly on bare rock (Fig. 4). It is easy to imagine that in such a situation a filial colony that is becoming independent must move, in order to build its own nest, to a different (not yet occupied) patch of vegetation – beyond a several-metre-wide belt of barren rock. In this way it moves away far from the zone penetrated by the maternal colony, and develops in isolation. With time there may develop hostile

relations, because there are no integrating factorts between the colonies. [In ants the development od hostile relations is very easy and this has been shown by experiments on artificial fissions of (highly polygynic) *F. exsecta* swarms (pers. unpubl. data). The phenomenon presented here (if it really exists) can be described as secondary monocaly.

Values of the index of aggressiveness towards alien conspecifics [measured by means of the PISARSKI (1973) method] displayed by the Finnish colonies of *F. exsecta* and by the Polish monocalic polygynic colonies of this species differ, in fact, only in respect of their range: for the former – 0–100% (PISARSKI, unpubl. data), for the latter – 40–50% (PISARSKI 1982c). What is more, the degree of aggressiveness of the Joskär *F. exsecta* colonies changes with time (PISARSKI, unpubl. data).

Within a polycalic colony, its particular members (colonies) are not, as a rule, aggressive to one another and yet sometimes they demonstrate some degree of mutual aggressiveness. This depends on the very extent to which the colonies have been integrated. The more isolated the foraging areas of particular colonies are and the weaker the exchange of food and workers is the greater the aggressiveness of individuals (!) (PISARSKI 1982c).

Scarcity of food – at least if recurring periodically – may be a factor that additionally increases aggressiveness between the *F. exsecta* colonies on Joskär. The foraging areas of these colonies cannot be considered rich. The sources of carbohydrate food there are provided by, unstable by nature, colonies of aphids on one or a few dwarf pine trees. Invertebrate fauna is very poor in the habitats where *F.*

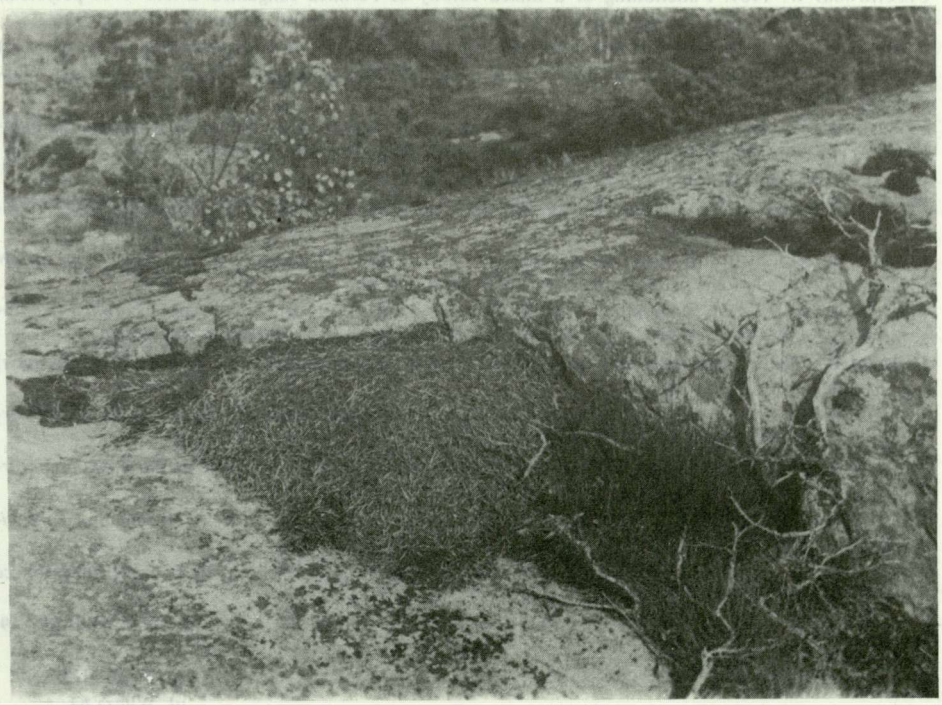

Fig. 4. *F. exsecta* colony on Joskär nesting in a rock crevice (Photo by W. CZECHOWSKI).

exsecta occurs. Ants find their main source of protein food in *Chironomidae* that appear in great masses but only from time to time, and then they become easy prey when trapped in the litter of juniper needles. For most of the season, however, ants must live under conditions bordering on starvation. In such a situation the competition (especially intraspecific) between colonies is more intensive. The ants under observation thriftily collected all the dead. This may be an indication that they were short of food. Under favourable trophic conditions dead bodies are left on the battlefield.

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

STRESZCZENIE

Konflikt wewnątrzgatunkowy u *Formica exsecta* Nyl. (*Hymenoptera, Formicidae*)

Opisany jest kilkudniowy konflikt między dwoma monokalicznymi mrowiskami *Formica exsecta* Nyl., których zasięgi penetracji normalnie nie stykały się. Konflikt został sprowokowany eksperymentalnie przez wyłożenie karmników w strefie niczyjej, rozdzielającej terytoria mrowisk. Walki mrówek były bardzo zaciekłe, w końcowej fazie jedno z mrowisk nieomal zaatakowało gniazdo drugiego, po czym sytuacja wróciła do normy. Obserwacje przeprowadzono na wyspie Joskär w Archipelagu Tvärminne (południowa Finlandia). Prześledzone zjawisko przedyskutowano w kontekście biologii gatunku na tle specyfiki lokalnych warunków siedliskowych.