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Competition between *Formica exsecta* NYL. and *Formica pressilabris* NYL. (*Hymenoptera, Formicidae*)

[With 4 figures in the text]

Introduction

Formica exsecta NYL. and *Formica pressilabris* NYL. are the most common species of the palaearctic subgenus *Coptoformica* but they are not frequently met in Poland. *F. pressilabris* is even thought to be a rare species.

F. exsecta occurs in the northern part of the Palaearctic Region, while the range of *F. pressilabris* is considerably more limited. The latter species inhabits central, northern and eastern Europe. It is also rather numerous in the mountains of southeastern Europe. The range of both the species in the mountains reaches the lower boundary of the lower mountain forest (DLUSSKY 1967, DLUSSKY and PISARSKI 1971, PISARSKI 1962).

In Poland, *F. exsecta* is the most abundant in the eastern part of the country. Isolated stands also occur in central and northwestern Poland. In southwestern regions this species was not recorded almost at all. *F. pressilabris* is considerably less common in Poland. Sparse, separated stands of this species were found only in eastern and northern Poland (DLUSSKY and PISARSKI 1971, PISARSKI 1962).

The colonies of *F. exsecta* and *F. pressilabris* are generally situated in dry, exposed to the sun areas, but they can also be found in moist habitats (STITZ 1939, DLUSSKY and PISARSKI 1971). Both these species represent typical ecotonal forms, mainly inhabiting the edges of shrub areas or forests of different types, and clearings. They also occur in loose, light second growth (DLUSSKY and PISARSKI 1971).

The morphology, ethology and ecology of both these species are very similar. But only the workers have similar morphology, the sexual forms being different. *F. exsecta* is slightly larger but it is rather difficult to distinguish both these species by eye in the field. What is more, they build identical nests. It is also characteristic that in the Bieszczady Mts. *F. exsecta* and *F. pressilabris* occupy identical or similar habitats.

Occurrence in the Bieszczady. *F. exsecta* and *F. pressilabris* are characteristic species of meadows and pastures. These habitats are man-made grasslands which replaced the original forests, and the management of which is not continued. Now a succession of the vegetation takes place there. In addition, *F. exsecta* was found in clearings of mixed forests and in light spruce and larch second growth (Dlussky and Pisarski 1971, Parapura and Pisarski 1971). A characteristic feature of the colonies occupying these habitats are numerous traces of deserted nests in the places shadowed by growing trees. Gradual succession of woody plants in the grasslands originally occupied by the species of the subgenus *Coptoformica* is followed by the succession of forest ants of the subgenus *Formica* s. str. such as *F. rufa* L. or *F. polyctena* Foerst.

Nests. Both the species of ants build identical nests with the aboveground part in the form of a mound composed of plant remains. Generally the permanent nests of *F. exsecta* are 20–30 cm in diameter, although considerably larger constructions are also met with. The nests of *F. pressilabris* are usually a little smaller, their diameter being 15–20 cm. Larger nest of this species are rare. The diameter of the largest nest of *F. exsecta* found in the Bieszczady was 1.1 m. It was situated in a large polycalic colony. The largest nest of *F. pressilabris* was about 1 m in diameter. It was found in a meadow located along the Wołosaty stream, near the Bereżki village. This nest was occupied by a monocalic colony. Both these nests of unusual sizes were almost flat (about 15 cm high).

Mono- and polycalism. *F. exsecta* and *F. pressilabris* form both monocalic and very large polycalic colonies in the Bieszczady Mts. The colonies of *F. exsecta* are particularly well developed. They frequently consist of more than 100 nests and occupy an area of thousands square meters. The colonies of *F. pressilabris* are generally smaller, but two exceptionally large, composed of several dozen nests each, were found in the Bieszczady (Czechowski 1975). The numbers of individuals in the nests of *F. exsecta* vary from 1,000 to 10,000 (Stitz 1939). In the Bieszczady many nests of this species are occupied by considerably larger numbers of individuals of an order of many thousand individuals. The numbers of ants in the nests of *F. pressilabris* are considerably smaller; generally several thousand individuals live in a nest (Czechowski 1975).

Social structure. Two types of social structure can be distinguished in most species of the subgenus *Coptoformica*. Particular swarms can be mono- or polygynic. Some ethological characteristics of the swarm are related to

the type of social structure (PISARSKI 1973). In the Bieszczady the *F. exsecta* societies of both types occur, although monogynic colonies are considerably less numerous. All *F. pressilabris* societies found in the study areas were of polygynic character, but the existence of monogynic colonies of this species can not be excluded.

Occurrence of these two closely related species in the same habitats, even in immediate vicinity, coupled with an identical ethology and habitat requirements, as it might seem at first sight, accounted for a need to analyse the character of interrelations between them, and to find specific features which diversify they ecological niches.

Subject and methods

The study was carried out near the village Ustrzyki Górne in the Bieszczady Mts. during June–September of 1971 and 1972. In this region the colonies of *F. pressilabris* are rather frequently met in vicinity to very abundant colonies of *F. exsecta*. Several polycalic colonies and many separate nests of both species were observed. Also some observations made in this area by Dr. B. PISARSKI in 1967–1970 are included.

A number of nest artificially moved to another place were observed. The method of artificial colonization consists in the removing of a part of the nest materials, with large numbers of workers, larvae and pupae, from a well developed nest into a new place. The artificial nest can develop only if it is placed in a suitable habitat. If the removal is done on a hot, sunny day (especially, after a prolonged period of unfavourable weather conditions), there is a great probability of removing some females. The behaviour of ants removed without a fertile female does not differ from normal one, but such colony can exist only one season.

Because well developed nests of *F. pressilabris* were rare in the study area, and the response of this species to the destruction of the nest is very specific, the method of artificial colonization could not be extensively applied. After a short period of irritation and aggressiveness, the ants retired to the belowground part of the nest, and it was not possible to catch an appropriate number of individuals. For this reason only one variant of the original, more extensive experiment was carried out. It was an artificial introduction of a *F. exsecta* colony into the area of a *F. pressilabris* polycalic colony. A reverse combination was not possible because of the reasons mentioned above. Changes in the range of penetration of the introduced colony of *F. exsecta* and changes in the densities of both competing species in their territories were recorded every seven days using a biocoenometric frame 0.25 m^2 in area.

The artificial nests of *F. exsecta* and *F. pressilabris* were also established in close vicinity to each other, at a distance of 1 m, in neutral, almost typical

of this species habitats. Regular observations of such pairs of nests made it possible to deliminate the boundary between the territories occupied by each of these species, to observe the changes in the size of these territories with time and also the behaviour of ants of both species in direct contacts.

To estimate the relative numbers of individuals per nests, the marking and recapture method was used. The abdominal terga of ants caught were marked with small spots of "Wilbra" lacquer which is used to colour leather. All ants present on the nest surface in the area delimited by a wire hoop 15 cm in diameter were captured during five minutes. All individuals caught were placed during sampling in a high plastic container the edges of which were moistened with paraffin oil. When the sampling was completed they were marked and released on the nest surface. Relative numbers of ants per nest were calculated from the Lincoln formula (AYRE 1962, CHEW 1959 and 1960, CZEN and DŻAN 1961, PĘTAL and PISARSKI 1966):

$$N = \frac{Tn+1}{t+1},$$

where T is the number of marked individuals, n is the number of all individuals caught per samples, and t is the number of marked individuals which were recaptured.

Competition under natural conditions

During the study period the societies of *F. exsecta* and *F. pressilabris* were never located so close to each other that their territories around the nests could adjoing. But in preceding years PISARSKI (personal communication) found some nests of *F. pressilabris* within the area occupied by a very extensive colony of *F. exsecta* in the Ustrzyki Górne region. Numerous colonies of aphids on the vegetation, rich insect community and inaccessibility of the area provided excelent conditions for ants. The dynamic polycalic colony of *F. exsecta*, rapidly increasing in numbers, probably eliminated weaker societies of *F. pressilabris*. In 1972 the workers of this *F. exsecta* society attacked a very frequented food-way of *F. pratensis* RETZ., which passed along the border of the colony from the nest situated near the *F. exsecta* colony. By the time of this aggression any conflicts between these societies were not observed. Therefore, it can be suggested that a certain relatively impassable boundary was formed between the territories of these two competing species, and it was respected by *F. exsecta*, which is the dominant in this area, by the time when the number of individuals in its colony reached a treshold level. Probably in the same way a colony of *F. pressilabris* was eliminated earlier.

An opposite process occurred in an open, exposed to the sun clearing with scarce food resources, where the colonies of both *Coptoformica* species

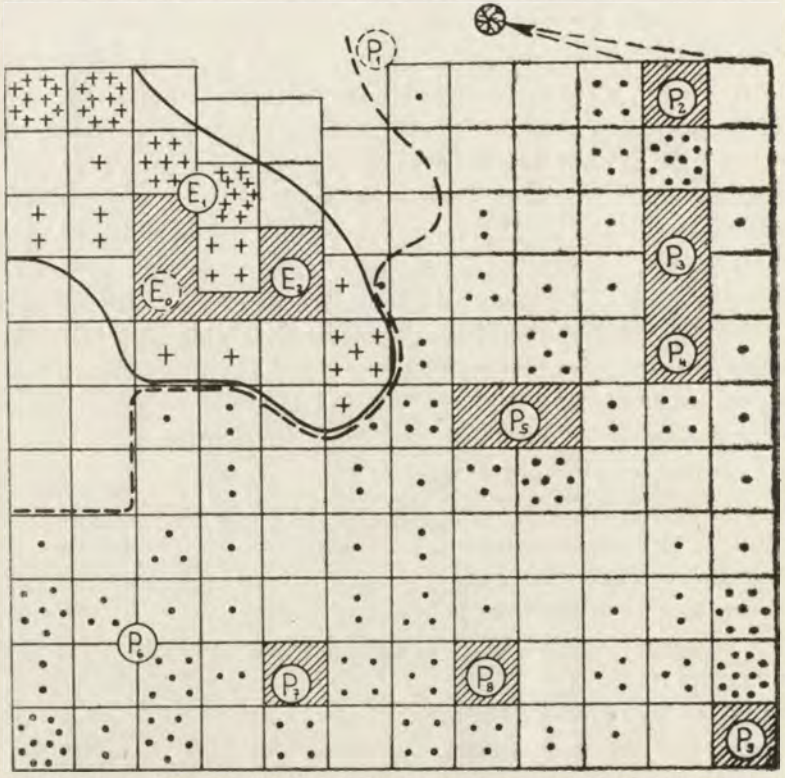
were situated in vicinity to each other, under the same environmental conditions. The colony of *F. pressilabris* consisted of about 20 nests with a diameter of about 10–15 cm. *F. exsecta* occupied two nests at a small distance, with a diameter of 25 cm each. The observations were made every year since 1967 (PISARSKI in litt.). *F. pressilabris* frequently moved from one nest to another and the numbers of individuals in their nests varied. Because some nests were left and another established at the same time, the total activity of the colony remained stable. In *F. exsecta*, however, new nests were not established, and already existing ones continuously died out. In 1972 only one nest of this species was occupied, and it could be expected that this was the last season of its existence. The nest was damaged and only several ants walked on its surface. Even the scattering of the nest was not followed by a normal response of ants, the total number of which was several dozen. Because the density of *F. pressilabris* on the territory of *F. exsecta* was low, and the distance between both colonies was large, an active elimination of *F. exsecta* by the competing species can not be taken into account. Rather habitat conditions were unfavourable for *F. exsecta*.

The observations of numerous colonies of both these *Coptoformica* species suggest that *F. exsecta* can live in rich, undisturbed habitats, while *F. pressilabris* can also survive in the habitats of poor trophy. For instance, a well developed colony of *F. exsecta*, composed of several very large nests (30–40 cm in diameter) died out when this area was grazed by sheep and cattle. At the same time in other areas under identical habitat conditions existed rather well developed colonies of *F. pressilabris*. Specific features of *F. pressilabris* bionomics, which enable this species to adapt to unfavourable environmental conditions are discussed below.

Competition under experimental conditions

To find which of the species under study has greater physical advantage over its competitor, the nests of *F. exsecta* and *F. pressilabris* were experimentally established in close vicinity. They consisted of similar numbers of individuals. Always the same behavioural pattern was observed in this experiment. The direct contacts between the individuals of both species was immediately followed by a fight of 2–3 hours, then a boundary was established and it was respected by both species. The hostile ants meeting each other along this boundary suddenly jumped back to avoid the fight. The numbers of killed individuals were similar on both sides. But in all cases, *F. pressilabris* societies, despite of an apparent stability, moved after several days to another place, outside of the zone of direct contacts with *F. exsecta*.

The way of fight between ants of the subgenus *Coptoformica* is very characteristic. They catch an adversor with mandibles from the above, between the head and the thorax, and slowly decapitate it.



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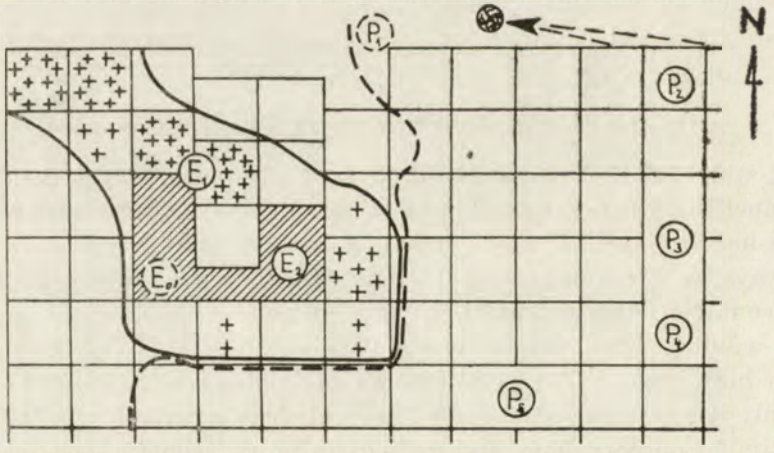

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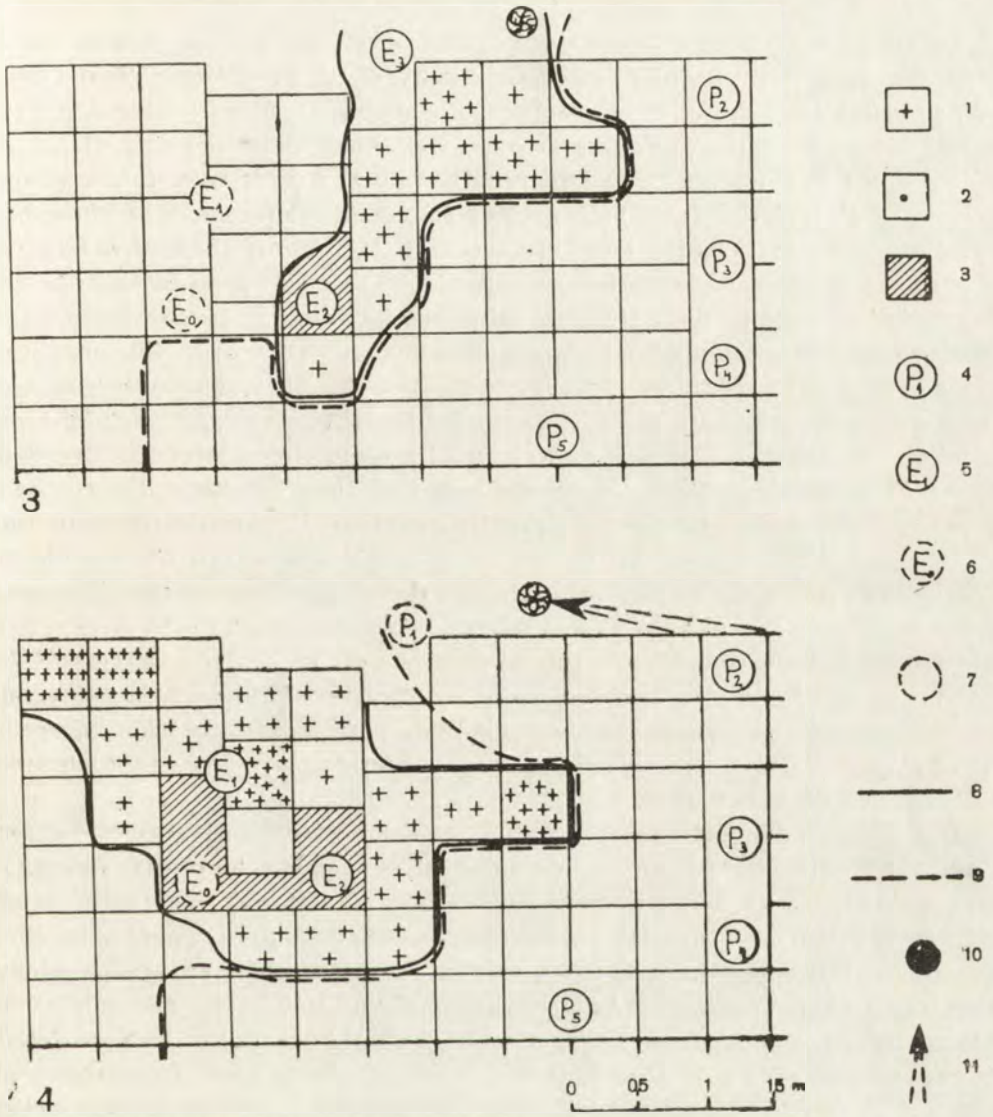

Fig. 1–4. Territory of the *F. exsecta* colony introduced into the area of a polycalic colony of *F. pressilabris*, and the densities of both species; 1 – 1 July, 1972; 2 – 8 July, 1972; 3 – 15 July, 1972; 4 – 22 July, 1972. (Explanation of symbols: 1 – density of *F. exsecta* per 0.25 m²; 2 – density of *F. pressilabris* per 0.25 m²; 3 – area near the nest with a high density of ants; 4 – nest of *F. pressilabris*; 5 – nest of *F. exsecta*; 6 – area of the experimental introduction of *F. exsecta* colony; 7 – deserted nest; 8 – boundary of the territory of *F. exsecta*; 9 – boundary of the territory of *F. pressilabris*; 10 – source of food; 11 – foraging-way).

In another type of experimental colonization, *F. exsecta* swarms were introduced into the area of a polycalic colony of *F. pressilabris*. Two types of *F. pressilabris* response were observed, depending on force relations. When the number of introduced *F. exsecta* was small, they were violently attacked by ants from the nearest nests and repidly killed. All attemps to introduce a society of *F. pressilabris* into the area of *F. exsecta* colony ended in the same way. But when sufficiently large numbers of *F. exsecta*, slightly exceeding the numbers of hosts, were introduced into the area of a *F. pressilabris* policalic colony, the response of the latter was different. Irritated *F. pressilabris* approached the hostile nest only to a certain distance, and they only did not allow the ants running about to come nearer to their nests. Although the introduced ants were under unfavourable conditions for the first days after establishing the nest, they reached stability soon, generally occupying one of the deserted nest of *F. pressilabris*. Then, *F. exsecta* enlarged their territory due to their aggressive behaviour, and they frequently repulsed *F. pressilabris* from the nearest nests. For instance, an introduction of *F. exsecta* into the middle of a polycalic *F. pressilabris* colony resulted in a desertion of the nearest *F. pressilabris* nest. Their inhabitants moved to one of more distant nests, which was indicated by a rapid increase in the density of ants in it. This swarms of *F. exsecta* died out in the next season probably because of the lack of a female. This experiment was repeated in the same place next season. Another adjacent nest of *F. pressilabris* was deserted and its inhabitants moved to a nest situated at a distance of about 1 m.

In the cases, when the territories around the nests of both species did not adjoin, the fights were frequently observed at the points where their foraging-ways crossed, particularly, in the places where a joint way ran to the same food source. Also in such case *F. exsecta* dominated. For instance, a conflict was observed between two societies in the situation when an aphid colony living on an alder buckthorn (*Frangula alnus* Mill.) shrub, was the only available source of carbohydrate food. After a several-hour fight, *F. pressilabris* retired, and two days later they moved to another, empty nest. The introduced swarm of *F. exsecta* was maintained by the next season, only its position being slightly changed several times. The results of this experiment are shown in Figs. 1–4. The records were made at weekly intervals. The territory of *F. exsecta* was gradually expanded towards the source of food and, at the same time, *F. pressilabris* were expelled from their foraging area. The relative number of individuals in *F. exsecta* colony, found by marking and recapture method, was 1,300, while that of nearby *F. pressilabris* nests was 500–700 individuals. These figures, however, are not fully comparable because the *F. exsecta* nest was under intensive construction at that time, and greater than usually numbers of individuals were caught on the surface. It can be assumed that the real numbers of individuals were similar in all adjoining nests.

Structure of polycalic colonies of *F. exsecta* and *F. pressilabris*

Components of such complex systems as polycalic ant colonies must be functionally and morphologically specialized to function in a proper way. Functional specialization is particularly pronounced in typical colonies of ants of the subgenus *Formica* s. str. (ZAKHAROV 1972). Typical, wide-spread polycalic colonies of *F. exsecta* and *F. pressilabris* are also composed of different types of nests. The most important are permanent nests of two kinds – maternal and derived (branches), and also temporary nests, called stations or food branches. Maternal nests are responsible for reproduction, young generation development, and production of sexual forms. From time to time groups of individuals leave these nests to establish derived colonies. Stations (food branches) are small, primitive nests, without belowground parts, inhabited by small groups of workers (without females and offspring) temporarily isolated from permanent nests. They are situated close to the sources of food, and enable the society to use economically trophic resources (PISARSKI 1973, CZECHOWSKI 1975).

Detailed analysis of the structure of polycalic colonies of both species in different habitats shows considerable differences between them. The colonies of *F. pressilabris* in destructed or poor habitats (most *F. pressilabris* societies occupies such habitats in the Bieszczady) are considerably more dispersed than those of *F. exsecta* living under the same conditions. The societies of *F. pressilabris* consist of many small permanent nests situated close to each other, and of many stations covering the territory of a colony with a dense net. The stations are frequently moved from one place to another with the exhausting of successive food resources. Even mature and stabilized societies of *F. pressilabris* can change the colony structure when food conditions deteriorate. It can be seen from the fact that many large nests are deserted in the habitats where dispersed colonies are met now (CZECHOWSKI 1975, Figs. 7, 8, 9 and 10).

Different behaviour is observed in the societies of *F. pressilabris* living in habitats with rich food supply (in the study area such situations were rare). The nests of monocalic colonies are very large (about 30 cm in diameter) and occupied by well developed swarms. Polycalic colonies consist of relatively few but very large nests situated far from each other. The distance between the nests in the colonies of *F. pressilabris* living in poor habitats is several dozen centimeters, and in rich habitats it is several meters.

Both mono- and polycalic societies of *F. exsecta* in the Bieszczady generally occupy the habitats rich in carbohydrate and protein food. Although the structure and function of particular nests in the colonies of these species are also diversified, the ecological plasticity of *F. exsecta* seems to be lower. When

trophic conditions considerably deteriorate, the colonies of *F. exsecta* can not adapt to a new situation, and they die out gradually, while the colonies of *F. pressilabris* do not. Occasionally derived nests and stations can be formed but they are sparse and weak.

Food requirements in *F. exsecta* and *F. pressilabris*

Like most ant species, both *Coptoformica* species use carbohydrate and protein food. The carbohydrate food is provided by aphids in the form of honeydew. Aphid colonies living on stems of herbs, shrubs and trees are actively protected by these ants. Protein food includes small invertebrates, mainly small larval *Lepidoptera* and earthworms as they are easy to catch. *F. exsecta* is a more predatory species than *F. pressilabris*. A possibility of using this species in the biological protection of forests is even considered (DLUSSKY 1967, WESSELINOFF and HORSTMANN 1968). *F. pressilabris* is rather more specialized in using honeydew, at least in the societies under study. It is possible, however, that the differences in the diet between both species resulted from the differences between the habitats occupied by them; *F. exsecta* generally occupied more rich habitats than *F. pressilabris*.

These species of ants are not specialized in any definite aphid species and use those available at the moment. In the Bieszczady the following ant species are most frequently used by ants: *Chaitophorus leucomelas* KOCH, *Ch. truncatus* (HAUSM.), *Cinara pinea* (MORDV.), *C. stroyani* PAŠEK, *Brachycaudus cardui* (L.), *Microsiphum millefolii* WAHLGR., and, according to PISARSKI (1973): *Adelges tardus* DREYF., *C. laricis* (HART.), *C. boerneri* HRL., *C. bogdanowi* MORDV. and *Dysaphis sorbi* (KALT). *F. pressilabris* were met at the following aphid species: *Aphis chloris* KOCH, *A. frangulae* KALT., *B. cardui* (L.), *C. boerneri* HRL., and *Microsiphum* sp.[1]

Discussion of the results

As suggests PISARSKI (1973) in his study on *F. exsecta*, the aggressiveness of ant swarms decreases along a gradient from monogynic societies, through monocalic polygynic societies, to polycalic colonies, as a result of the loosening of social ties. The present results show that *F. pressilabris* is considerably less aggressive than *F. exsecta*, in the presence of both the prey and the man. This seems to be a direct result or relatively small densities of individuals in *F. pressilabris* societies on their territories, and in consequence by lower than in *F. exsecta* mutual stimulation through kinopsis (STÄGER 1931) or by excretion of alarm pheromones. It is also possible that lower aggressiveness of *F. pressilabris* can result from a tendency towards the division of the colony

[1] Aphids were identified by Prof. H. SZELĘGIEWICZ.

into many small swarms. This process could be respected as a further stage of the loosening of social ties. It is accompanied by a tendency towards the moving of the whole colonies to other places. Artificially established nests of *F. pressilabris* were moved on many times, even every several days, while the nest of *F. exsecta* were more stabilized in this area. Both these features of *F. pressilabris* bionomics (loosening of the social structurs and decrease in the nest stability) account for large possibilities of adaptation, which enable these ants to live under changing habitat conditions, and to invide new habitats, relatively scarce in food. On the other hand, because of the lower number of individuals in the nests and a decreased aggressiveness of *F. pressilabris*, this species is not so strong physically as *F. exsecta* and it is expelled by the latter from richer habitats.

In sum, general ethological and ecological similarities, such as environmental requirements and behaviour, enable *F. exsecta* and *F. pressilabris* to occupy the same habitats, but as a result of the differences in the bionomics between these species of *Coptoformica* they occur in a little different habitats. The common occurrence of so closely related ant species in the same habitats of the Bieszczady seems to be a transient phenomenon which is possible only due to the fact that these habitats are in the stage of ecological succession, they are not stabilized. Fauna of the Bieszczady meadows and pastures has not any stable characteristic species composition. When the stabilized stage is reached, these two species of ants will probably occupy different habitats.

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STRESZCZENIE

[Tytuł: Konkurencja między *Formica exsecta* Nyl. i *Formica pressilabris* Nyl. (*Hymenoptera, Formicidae*)]

Formica exsecta i *Formica pressilabris*, należące do podrodzaju *Coptoformica*, są mrówkami o bardzo zbliżonej morfologii, etologii i ekologii. W Bieszczadach obydwa gatunki występują w tych samych środowiskach, określanych jako „łąki i pastwiska na dawnych terenach uprawnych". Są to środowiska sukcesyjne o nie ustalonym jeszcze składzie faunistycznym i prawdopodobnie dlatego oba gatunki o niemalże jednakowych wymaganiach ekologicznych mogą występować obok siebie. Należy sądzić, że w miarę stabilizacji tych terenów będzie następował podział siedlisk między oba gatunki *Coptoformica*.

Celem niniejszych badań było znalezienie tych cech bionomii obu gatunków mrówek, które różniąc je między sobą, pozwalają im bytować w tych samych środowiskach.

Obserwacje przeprowadzono w okolicy Ustrzyk Górnych (woj. krośnieńskie) i objęto nimi wiele mono- i polikalicznych społeczeństw *F. exsecta* i *F. pressilabris*.

Stwierdzono, że jakkolwiek potrzeby życiowe mrówek obu gatunków są mniej więcej jednakowe, to jednak *F. pressilabris* dzięki znacznym zdolnościom adaptacyjnym może z powodzeniem egzystować w siedliskach wyniszczonych, o małej zasobności pokarmowej, gdzie społeczeństwa *F. exsecta* nie mogą się utrzymać. Plastyczność ekologiczna *F. pressilabris* przejawia się dużą zdolnością do rozdrabniania społeczeństw na wiele małych i blisko siebie położonych mrowisk z chwilą pogorszenia się warunków siedliskowych. Gęsta sieć mało-

liczebnych mrowisk pokrywająca terytorium kolonii pozwala na ekonomiczne wykorzystanie skąpych zasobów pola troficznego.

Możliwości przystosowawcze *F. exsecta* są mniejsze, jednak rekompensuje to większa siła fizyczna i agresywność tych mrówek, dzięki czemu wypierają one społeczeństwa *F. pressilabris* z siedlisk pełnowartościowych.

РЕЗЮМЕ

[Заглавие: Межвидовая конкуренция у *Formica exsecta* Nyl. и *Formica pressilabris* Nyl. (*Hymenoptera, Formicidae*)]

Formica exsecta и *Formica pressilabris*, принадлежащие к подроду *Coptoformica*, очень близки друг к другу по своей морфологии, этологии и экологии. В Бещадах оба вида встречаются в одних и тех же биотопах, определяемых как „луга и пастбища на возделываемых в прошлом территориях". Повидимому, сукцессионный характер этих биотопов с неустановившимся окончательно фаунистическим комплексом дает возможность существовать тут одновременно двум видам, характеризующимся почти одинаковыми экологическими требованиями. Следует полагать, что по мере стабилизации этих территорий будет происходить также разделение биотопов между ними.

Автор поставил себе целью найти отличительные признаки в биономи обоих видов муравьев, которые позволяют им существовать в одних и тех же биотопах.

Наблюдения проведены в окрестностях Устжиков Гурных (Кросненское воеводство) и охватывают многие моно- и поликалические сообщества *F. exsecta* и *F. pressilabris*.

Констатировано, что, хотя экологические требования обоих видов муравьев более или менее одинаковы, то *F. pressilabris* благодаря значительным приспособительным способностям может с успехом существовать в биотопах бедных в кормовые ресурсы, в которых сообщества *F. exsecta* не были бы в состоянии удержаться. Экологическая пластичность *F. pressilabris* проявляется в способности к раздроблению сообществ на множество мелких и близко расположенных друг от друга муравеиников при ухудшении условий внешней среды. Густая сеть малочисленных колоний, покрывающих всю территорию, позволяет более рационально использовать скудные ресурсы кормового участка.

F. exsecta обладает меньшими приспособительными способностями, но благодаря большей физической силе и агрессивности вытеснят сообщества *F. pressilabris* из более полноценных биотопов.

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