

Bohdan PISARSKI, Kari VEPSÄLÄINEN

Competition hierarchies in ant communities (*Hymenoptera, Formicidae*)

[With 1 table and 2 figures in the text]

Abstract. A concept of competition hierarchy among ant species is presented. The hierarchy consists of three main levels, and the species are arranged in the hierarchy on the basis of social organization (mainly forager densities and recruitment efficiencies) of colonies. The concept allows testable predictions on probable and improbable species pairs in local ant species assemblages. Structure of competition hierarchy and positions of a number of North European species in it is reviewed. A schematisized map on minimal distances among nests of species belonging to various levels of the hierarchy is presented. A case study on relations among highest-level, territorial species, is described.

Introduction

As a majority of ant species are pantophages (omnivorous) and many are eurytopes, their ecological niches often overlap to a lesser or greater extent. It may lead to acute interspecific competition, often of the "contest" type (VEPSÄLÄINEN 1982). The probability that an ant colony is present depends partly on its position in the competition hierarchy (PISARSKI 1980, VEPSÄLÄINEN and PISARSKI 1982, SAVOLAINEN and VEPSÄLÄINEN 1988). The competition hierarchy is a conceptual frame, which allows predictions of locally probable and improbable species pairs (VEPSÄLÄINEN and PISARSKI 1982). Colonies (species) which occupy the highest position in the hierarchy are likely to live in profitable habitats. Species (colonies) which have lower positions in the hierarchy are pushed out to suboptimal habitats or their exploitation of the environment is limited by species (colonies) of higher rank in the hierarchy.

In this paper we first outline biological bases of competition hierarchy of ants. Then we describe relations among species belonging to different levels of the hierarchy and derive predictions on locally expected and unexpected species pairs. Relative locations (minimal distances) among nests of different-level species are featured in a schematisized map. A chapter on relations among highest-level species is followed by a case study, which tests predictions on species composition of local myrmecological assemblages.

Levels of competition hierarchies

The rank of a species (colony) in the competition hierarchy depends on its numbers and level of organization. When the numbers and organization are similar, size of workers may also be important.

Three fundamental levels can be distinguished in the competition hierarchy (VEPSÄLÄINEN and PISARSKI 1982). The lowest level (Group 1) is represented by species which defend only their nests ("nest territory"; BRIAN et al. 1965). The intermediate level (Group 2) consists of species which defend their nests and food sources ("food territory"; BRIAN et al. 1965). The highest level (Group 3) is occupied by species which defend the nest and the whole foraging area, i.e., territorial species.

Each level of the hierarchy is internally differentiated. As our studies of the competition hierarchy in ants have been carried out for a couple of years only, little data on internal differentiation of respective levels of the hierarchy is available and it concerns primarily Group 3.

Relations among species belonging to different levels of the hierarchy

The majority of European ant species belongs to Group 1, so it is the most varied one both in the taxonomy (all subfamilies and many genera are represented there) and behaviour (modes of nest building, effectiveness of forager recruitment, ways of foraging, habitat selectiveness, and ecological plasticity).

Species belonging to that group, e.g., of the genus *Myrmica* LATR., *Leptothorax* MAYR, *Formica fusca* L., form relatively small colonies of tens to several thousand of individuals; their workers are of 2.3 to 7 mm long. These species may found nests close to each other or even in contact to each other. It is possible because their workers are, as a rule, aggressive to the workers from other colonies only within the nest. Foraging areas of the colonies from this group may overlap and foragers from various colonies (species) may take use of the same sources of food. Conflicts between foragers from different colonies are

rare, however, for the places and ways of foraging are differentiated (e.g., *Myrmica scabrinodis* NYL. forages on soil surface and in the litter, and *Formica fusca* L. mainly in the upper layers of vegetation) and, probably, their diets are different. Moreover, the internal hierarchy of the group is likely to be of considerable importance. For instance, *Leptothorax acervorum* (FABR.) or *Formica fusca* L. workers forage individually and thus have a lower position in the competition hierarchy within the group. Usually they do not fight *Myrmica ruginodis* NYL. or *M. scabrinodis* NYL. ants which recruit rapidly large numbers of foragers to food sources, and which thus obtain a higher position in the hierarchy. For a more comprehensive review on interspecific differences in resource utilization, see BRIAN (1983).

Group 2 (species defending food source) consists of a lesser number of species among which there are many poly- or even eurytopes, and poly- or even pantophages [e.g., *Tetramorium caespitum* (L.), *Prenolepis imparis* SAY, *Camponotus ligniperdus* LATR., *Lasius niger* (L.)]. Workers of these species are 2.5 to 14 mm long, and they form colonies maximally of the order of 10^4 individuals. They are much more aggressive to alien individuals than the species of Group 1 so they can found nests only in a distance no less than several metres. Their foraging areas may partially overlap, but as they monopolize food sources and do not allow workers from other colonies (species) to make use of them, generally all food sources near the nest are occupied by the workers of that nest. There are only narrow passage areas between the neighbouring colonies in which food sources are made use of alternatively (BRIAN et al. 1965) and over which conflicts arise, which, however, are often ritual (PISARSKI 1980, CZECHOWSKI 1984), like in Group 3. There is no data on the internal hierarchy within this group. But it is conceivable that the stage of maturation (growth) of each colony, rather than the species status, defines its position in the hierarchy.

Group 3 (territorial species) is relatively coherent. In Central and North Europe there are a number of ant species which belong all to the *Formicinae* subfamily [the subgenera *Formica* s. str. L. and *Coptoformica* MÜLL., *Formica* (*Serviformica*) *cinerea* MAYR, *Lasius* (*Dendrolasius*) *fuliginosus* (LATR.)]. These are mostly relatively large (6 to 8 mm) species of forests and forest edges, which form colonies of 10^4 to 10^6 individuals. They all are pantophages but also active predators. Colonies of territorial species replace each other in space. Species of Group 2 can forage and found nests only on margins of territories extensively searched by a species of Group 3 (Fig. 1). Species of Group 1 can more freely forage and found nests in the foraging areas of territorial species, but then the species (colonies, individuals) are subordinated to the dominant, territorial one(s) (PISARSKI 1982). Periodically, usually in spring, there are fights among colonies of territorial species which, however, level out soon and aggression among workers of neighbouring colonies becomes ritualized (MABELIS 1979, PISARSKI 1982).

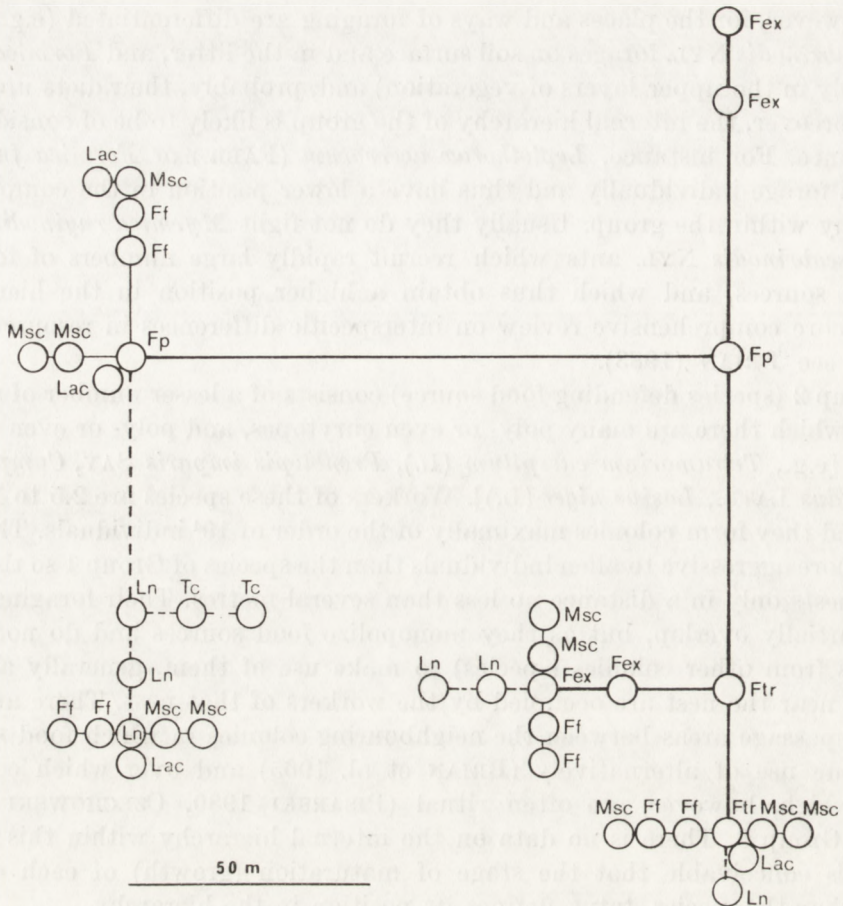


Fig. 1. Minimal distance between colonies of selected species belonging to different levels of the competition hierarchy. Species of 3rd level: Fp — *Formica polyctena* FOERST., Ftr — *F. truncorum* FABR., Fex — *F. exsecta* NYL.; species of 2nd level: Ln — *Lasius niger* (L.), Tc — *Tetramorium caespitum* (L.); species of 1st level: Msc — *Myrmica scabrinodis* NYL., Lac — *Leptothorax acervorum* (FABR.), Ff — *Formica fusca* L. [1st and 3rd level species on the basis of the authors' unpublished data, 2nd level species Ln and Tc according to BRIAN et al. (1965)].

Relations among the highest-level species

The internal hierarchy among the species of the highest level is clearly differentiated. Ranking of species has been studied in a South Finnish assembly of ants consisting of *Formica* (*F.*) *polyctena* FOERST., *F. (F.) truncorum* FABR., and *F. (C.) exsecta* NYL. The species differ in numbers and level of organization of the colony, and size of workers (Tab. 1).

Table 1. Characterization of 3rd level (territorial) ant species

| Species | Potential numbers of colony | Maximum worker size (mm) | Forager numbers on baits | Area of territory (m ²) |
|----------------------------------|-----------------------------|--------------------------|--------------------------|-------------------------------------|
| <i>Formica polyctena</i> FOERST. | 10 ⁶ | 9.0 | 100 | 20 000 |
| <i>Formica truncorum</i> FABR. | 10 ⁵ | 9.0 | 50 | 2 000 |
| <i>Formica exsecta</i> NYL. | 10 ⁴ | 7.5 | 20 | 200 |

F. polyctena FOERST. workers are big (4 to 9 mm), colonies are large, reaching to 10⁶ workers, and of a highly complicated structure and organization (ZAKHAROV 1972, 1973). Nests are very large (of 2 to 3 cubic metres) and foraging areas, covered with a route system, extend to over 1 ha. The density of workers on the foraging area is high and due to effective recruitment they forage very efficiently. The species often develops polycalic colonies. So numerous and having such energy-consuming structures (nest building and air conditioning, founding of routes), a colony requires great energy outlays and can thus exist only in extensive habitat patches of high food abundance and stability.

Workers of *F. truncorum* FABR. are of similar size, but the species forms much less numerous colonies of 10⁵ workers at most, which are of respectively simpler organization and smaller nests. The foraging area is considerably smaller and no clear-cut systems of routes are formed, only the preferred directions of foraging can be observed. The worker density near the nest is very high but it diminishes rapidly with distance and thus the effectively covered foraging area is much smaller than that of *F. polyctena* FOERST. Colonies of this species can exist in poorer, less stable habitats than do those of the latter species, e. g., early stages of forest succession. *F. truncorum* FABR. can form polycalic colonies which, probably, are able to compete with monocalic colonies of *F. polyctena* FOERST.

Workers of *F. exsecta* NYL. are considerably smaller than those of the two above-discussed species (5 to 7 mm). In the area under investigation (next chapter) it forms colonies amounting to 10⁴ workers (in good habitat conditions colonies of the species can amount to 10⁵ workers). The structure and organization of colonies is relatively simpler, its nests and foraging areas smaller, and practically devoid of routes. Density of workers in foraging area is not high and effectiveness of foraging much lower. It is a photophilous ecotonic species inhabiting also light forests. It can exist in relatively unstable habitats, in early stages of forest succession (e.g., in clearings sparsely covered with bushes, or in young forests). It is capable of forming polycalic colonies.

Forests in Central Europe are, as a rule, relatively young and small, and widely scattered. Their myrmecofauna is a successional one. Thus species typical for forests of the coniferous biome are the last ones to enter (e.g., *Formica rufa* L., *F. polyctena* FOERST.). As they generally do not saturate habitats dispersed with forests, other species may colonize them. Thus the relation between the species' position in the competition hierarchy and the habitat occupied is not so obvious in forests of Central Europe as it is in more mature North European forests.

A case study

Our research on the relations between species' positions in the competition hierarchy and structure of local ant species assemblages was carried out on the Joskär Island (Tvärminne archipelago) in the Finnish Baltic from 1980 till 1983. Joskär is a rocky island of an area of 10 ha. It is covered with vegetation of various levels of succession, from the earliest (open bare rock with small patches of lichens, mosses and grass at the top of the island and on cliff slopes), through large areas of juniper thicket ("scrub") and pine forest consisting of single pines and groups of pines separated by bare rock, to mature pine forest with well developed undergrowth of shrubs (the genera *Vaccinium* L., *Empetrum* L., *Calluna* SALISB., *Ledum* L.).

Joskär's open pine forest with an undergrowth area on rocks (1 ha) is entirely monopolized by a two-nest colony of *Formica polyctena* FOERST. which also includes 1 ha of rocks scattered with groups of pines (Fig. 2). A smaller pine forest with undergrowth is totally exploited by a *Formica lugubris* ZETT. colony. The remaining territorial species (*Formica truncorum* FABR. and *F. exsecta* NYL.) have been pushed by *F. polyctena* FOERST. and *F. lugubris* ZETT. out to poorer habitats (to rocks scattered with groups of pines and juniper thickets). *F. truncorum* FABR. and *F. exsecta* NYL. colonies which earlier occupied the area of the present *F. polyctena* FABR. territory, have been outcompeted (one *F. truncorum* colony was excluded during our investigations; as regards the other ones, only deserted ant-hills were left of them) (VEPSÄLÄINEN and PISARSKI 1982).

Almost all the remaining area of the island is covered by *Formica truncorum* FABR. and *F. exsecta* NYL. territories (Fig. 2). During our research *F. truncorum* FABR. began forming polycalic colonies and it increased its territories by outcompeting *F. exsecta* NYL. colonies (by driving them to extinction or by making them emigrate).

Lasius niger (L.) is the dominant species on those islands where the vegetation is in its earliest succession stages. On Joskär this species inhabits only small patches among territories of Group 3 species or outskirts of their foraging areas. It forms there large colonies which on their foraging areas tolerate only single foragers of species belonging to the highest hierarchical level and sometimes

conflicts occur there; they do not, however, allow other species of the second level of the hierarchy to found nests in their foraging area.

Colonies of Group 1 are distributed rather numerously on Joskär. They are tolerated by the territorial species, and excluding areas close to the nests of the latter species their density is rather high (SAVOLAINEN and VEPSÄLÄINEN 1988). The distances from the nest, kept clear of nests of first level species, are

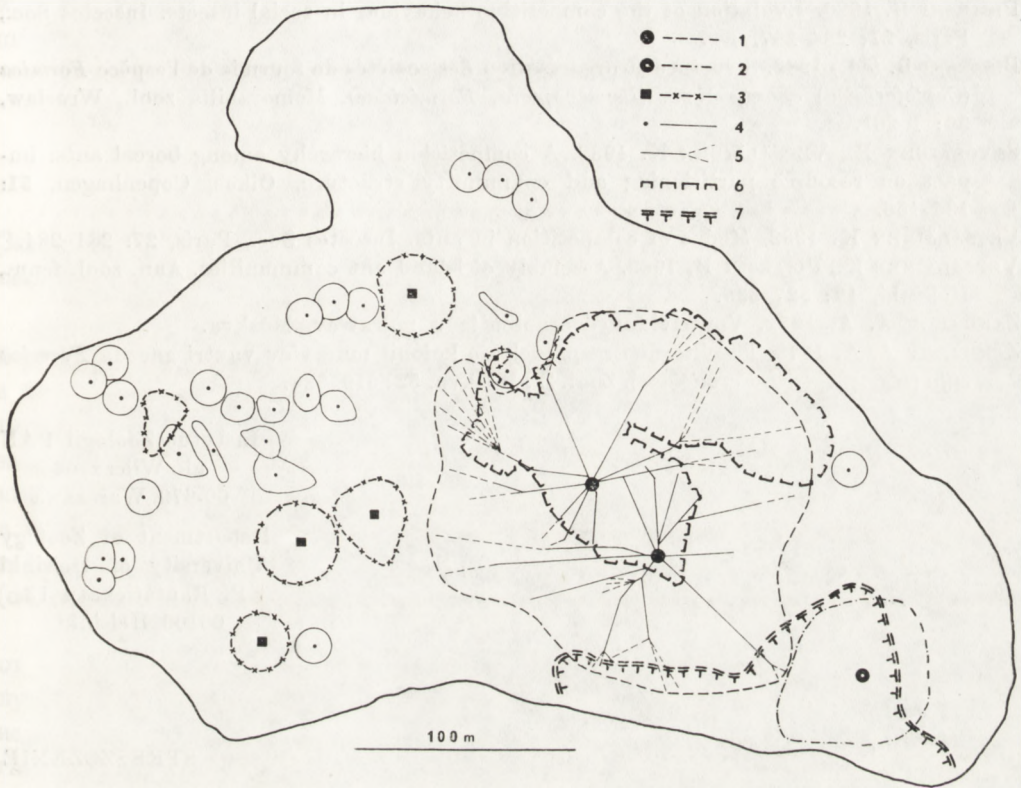


Fig. 2. Distribution of territorial ant colonies on the Joskär island; nests and borders of territories: 1 — *Formica polyctena* FOERST., 2 — *F. lugubris* ZETT., 3 — *F. truncorum* FABR., 4 — *F. exsecta* NYL.; 5 — routes of *F. polyctena*; 6 and 7 — pine forests with undergrowth.

for *Formica exsecta* NYL. about 1 m, for *F. truncorum* FABR. about 1.5 m, and for *F. polyctena* FOERST. about 5 m (Fig. 1). Group 1 species may coexist with territorial species because potential foraging area of the latter usually is ten times the minimum realized one, so during periods of food abundance it is enough for the third and first level species. And because the latter “subordinate” they do not stir the aggression of the host and both their foragers and concealed (ground) nests are tolerated.

REFERENCES

- BRIAN M. V. 1983. Social Insects. Chapman and Hall, London.
- BRIAN M. V., HIBBLE J., STRADLING D. J. 1965. Ant pattern and density in a southern English heat. *J. anim. Ecol.*, Oxford, **34**: 545-555.
- CZECHOWSKI W. 1984. Tournaments and raids in *Lasius niger* (L.) (*Hymenoptera, Formicidae*). *Ann. zool.*, Warszawa, **38**: 81-91.
- MABELIS A. A. 1979. Wood ant wars. The relationship between aggression and predation in the red wood ant (*Formica polyctena* FÖRST.). *Netherl. J. Zool.*, Leyden, **29**: 451-620.
- PISARSKI B. 1980. Evolution of the competitive behaviour in social insects. *Insectes Soc.*, Paris, **27**: 284-287.
- PISARSKI B. (ed.) 1982. Structure et organisation des sociétés de fourmis de l'espèce *Formica (Coptoformica) exsecta* NYL. (*Hymenoptera, Formicidae*). *Memorabilia zool.*, Wrocław, **38**: 1-281.
- SAVOLAINEN R., VEPSÄLÄINEN K. 1988. A competition hierarchy among boreal ants: impact on resource partitioning and community structure. *Oikos*, Copenhagen, **51**: 135-155.
- VEPSÄLÄINEN K. 1982. Modes of competition in ants. *Insectes Soc.*, Paris, **27**: 281-284.
- VEPSÄLÄINEN K., PISARSKI B. 1982. Assembly of island ant communities. *Ann. zool. fenn.*, Helsinki, **19**: 327-335.
- ZAKHAROV A. A. 1972. Vnutrividovye otnošenija u murav'ev. Moskva.
- ZAKHAROV A. A. 1973. Posekturnoe raspredelenie kolonii murav'ev vnutri gnezda *Formica rufa* (*Hymenoptera, Formicidae*). *Zool. Ž.*, Moskva, **52**: 519-524.

Instytut Zoologii PAN
ul. Wilcza 64
00-679 Warszawa

Department of Zoology
University of Helsinki
P. Rautatiekatu 13
00100 Helsinki

STRESZCZENIE

[Tytuł: Hierarchia konkurencji w zespołach mrówek (*Hymenoptera, Formicidae*)]

Większość gatunków mrówek to pantofagi, a wiele — eurytopy, w związku z czym nisze ekologiczne wielu gatunków mrówek zachodzą na siebie w mniejszym lub większym stopniu. Prowadzi to do ostrej konkurencji międzygatunkowej, często typu „contest”. Możliwość zajęcia niszy ekologicznej przez społeczeństwo mrówek zależy od jego pozycji w hierarchii konkurencji. Najbogatsze nisze ekologiczne zajmowane są przez gatunki (społeczeństwa) zajmujące najwyższą pozycję w hierarchii. Gatunki zajmujące niższe pozycje w hierarchii są wypierane do uboższych nisz, lub też eksploatacja przez nie niszy jest ograniczana przez gatunki (społeczeństwa) zajmujące wyższą pozycję w hierarchii.

Miejsce, jakie gatunek (społeczeństwo) zajmuje w hierarchii konkurencji, zależy od liczebności osiągananej przez jego społeczeństwa oraz od stopnia rozwoju

ich organizacji. Na podstawie dotychczasowych danych możemy wyróżnić 3 podstawowe poziomy hierarchii. Najniższy (grupa I) tworzą gatunki broniące jedynie gniazda. Poziom środkowy (grupa II) — gatunki broniące gniazda i źródeł pokarmu. Poziom najwyższy (grupa III) — gatunki broniące gniazda wraz z całym polem troficznym. Minimalna odległość między mrowiskami poszczególnych gatunków zależy od ich pozycji w hierarchii konkurencji i jest największa pomiędzy mrowiskami grupy III. Ponadto odległość między mrowiskami gatunków należących do tej samej grupy jest zwykle większa niż pomiędzy mrowiskami gatunków z różnych grup.

РЕЗЮМЕ

[Заглавие: Иерархия конкуренции в сообществах муравьев (*Hymenoptera, Formicidae*)]

Большинство видов муравьев являются пантофагами, а многие эвритопами. В связи с этим экологические ниши многих видов муравьев находят друг на друга в большей или меньшей степени. Это ведет к острой межвидовой борьбе, часто типа „contest”. Возможность занятия обществом муравьев экологической ниши зависит от его позиции в иерархии конкуренции. Наиболее богатые экологические ниши занимают виды (общества) находящиеся на наиболее высокой позиции в иерархии. Виды, занимающие в иерархии более низкое положение, вытесняются в более бедные ниши или же использование ими ниши ограничивается видами (обществами) занимающими более высокое положение в иерархии.

Место, которое занимает вид (общество) в иерархии конкуренции, зависит от его численности, а также от степени развития организации. На основании полученных до настоящего времени данных можно выделить три основные уровня иерархии. Самый низкий (I группа) составляют виды, которые защищают только гнезда. Средний уровень (II группа) — виды защищающие гнезда и источники корма. Наиболее высокий уровень (III группа) — виды защищающие гнезда и все трофическое поле. Минимальное расстояние между муравейниками отдельных видов зависит от их позиции в иерархии конкуренции и больше всего между муравейниками III группы. Кроме того расстояние между муравейниками видов, принадлежащих к одной и той же группе, обычно больше, чем расстояние между муравейниками муравьев из разных групп.