

**Plasticity of the foraging strategy in non-territorial ant
species (Hymenoptera: Formicidae)**

– summary of the PhD-thesis –

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Szeged (Hungary)
2005

THEORETICAL BACKGROUNDS AND HYPOTHESES

Ants are amongst the most successful insect groups due to their eusocial way of life, because their adaptability to different type of habitats depends largely on the plasticity of their social system, as well as on the efficiency of their foraging strategies (Sudd and Franks 1987, Hölldobler and Wilson 1990). The more plastic a foraging strategy is, the more adaptable a colony becomes to changing conditions, which increases its chance to survive (Pasteels et al. 1987a, b). The simplest way of foraging is searching for food and retrieving it individually (Beckers et al. 1989). Large food sources, nevertheless, require the co-operation of several individuals. The retrieval of such sources is made possible through the active recruitment of other foragers by the discoverer (de Biseau et al. 1994, Jarau et al. 2003). This allows the rapid exploitation of a source, and, last but not the least, it secures to food source against rival species (Slaa et al. 2003).

Three types of recruitment strategies are known in ants, which can successively occur in the same species:

(1) Tandem running is the simplest way: the discoverer recruits actively at the colony, and on turning back to the source it is followed closely by one or two individuals, which keep direct contact with the leader ant all the way to the source.

(2) During group-recruitment the foragers are also recruited directly by the discoverer, nevertheless they follow the recruiter on a pheromone-trail laid by it, without having any direct contact during their way to the source.

(3) The most efficient is the mass recruitment, which is generally preceded by group-recruitment. The recruitment of foragers can occur indirectly through the increasing concentration of the pheromone on the trail leading to the food source.

Optimality and plasticity

Foraging individuals make several choices during foraging, e.g. when and where to forage, and what to search for. Choices can be made on the basis of innate preferences or previous experiences (so-called *personal information*), as well as information got from nestmates (so-called *public information*) can also serve as basis for decisions made during the foraging process (Bonabeau et al. 1998, Wehner et al. 2004). Presumably foragers try to optimize by obtaining more profit with less foraging cost. The distance of the food source seems to be the most obvious factor that needs to be optimized (Detrain et al. 1999, Torres-Contreras and Vasquez 2004), as well as the size and quality of food (Detrain et al. 1999, Mailleux et al. 2003, Cogni and Oliveira 2004), but other important factors should also be taken into consideration as the size of the colony, or the competitive and predatory pressure (Pasteels et al. 1987b, Thomas and Framenau 2005).

It seems logical that individual optimization results in optimal pattern on colony level, and vice versa. Nevertheless individual decisions are the result of a trade-off: a compromise between immediate optimization on individual level and long-term benefit on colony level realized through collective exploitation (Detrain et al. 1999). The interest of the individual is to spend as many time as possible at to food source to maximize the net benefit/cost ratio, but the interest of the colony is his rapid return in order to recruit others to the exploitation of the food source.

Complex collective patterns can emerge from the interplay of simple individual behaviours, or/and from the interaction between them and their environment as self-

organization theory predicts (Pasteels et al. 1987a, b, Camazine et al. 2001). The possibility of error is very important, as trail-following mistakes emerging from inaccurate communication can cause the discovery of other sources dispersed in the vicinity of the already discovered food pile (Pasteels et al. 1987a, b). Positive feedback is also an important feature of self-organized patterns, as it plays a decisive role in choosing the best source when two sources of different quality are present simultaneously. Foragers coming from the best source are recruiting more intensely, which causes an increasing difference in the exploitation rates of the two sources (Pasteels et al. 1987a, Mailleux et al. 2003, Cogni and Oliveira 2004). Negative feedback is also important (Bonabeau et al. 1998): recruitment ceases to an overcrowded source as foragers bump into each other with increasing frequency, which reduces trail-laying and recruiting behaviour significantly.

Competition and foraging strategies

The majority of ants are polyphagous, and considerable niche-overlap can occur among them, which causes strong inter- and intraspecific competition. The coexistence of rival species is supported even by differences in their foraging strategies (Vepsäläinen and Savolainen 1990, Gallé 1994, Gallé et al. 1994, Jarau et al. 2003). Ants can be arranged in a linear competition hierarchy on the basis of the colonies' social organization and foraging characteristics (Vepsäläinen and Savolainen 1990): (1) *submissive* species, which defend only their colony, (2) while *aggressive* species defend their food sources, as well, (3) and *territorial* species sustain and defend a territory.

Plasticity of non-territorial ant species – questions and hypotheses

Territorial species are the organizing centers of ant communities. They influence the quantity, quality and availability of food sources, and generally the foraging strategy of other non-territorial ant species. It is plausible to assume that the key to the success of non-territorial species is a certain degree of plasticity, which makes possible their continuous adaptation to changing ant-community conditions (Pasteels et al. 1987a, b, Detrain et al. 1999).

The foraging strategy of a given ant species can be properly understood only by taking account of the ecological context in which it is displayed. In the lack of such analysis an erroneous picture can be formed easily (Savolainen and Vepsäläinen 1989, Detrain et al. 1999, Cogni and Oliveira 2004). Our experiments were carried out in field-conditions in order to ensure the proper ecological context. The hypotheses of this study can be summarized as follows:

- The colony maximizes the probability of food discovery.
- The spatial distribution of foragers around a colony predicts the discovery and exploitation pattern of food sources.
- Colonies prefer close sources to distant ones.
- Colonies of non-territorial species do not influence negatively the distribution of other species.
- Non-territorial species always behave accordingly to their status.
- Non-territorial species behave in the same way behaviour under any ant-community circumstances.

MATERIALS AND METHODS

Species

Myrmica rubra (Linnaeus, 1758) is one of the most common European ant species. It occurs in forests in plains and hilly regions, and on wet pastures, marshlands in the mountains (Markó et al. 2004). It is a non-territorial, submissive species (Savolainen and Vepsäläinen 1989). It was studied in Romania, in a mixed oak forest near Cluj-Napoca (four colonies), and at the margin of a mixed forest near the Bezdin monastery (four colonies) in summer 2000.

Myrmica ruginodis Nylander, 1846 prefers colder and dumper habitats, it occurs mostly in forests in the hilly region and in the mountains, but also on mountain pastures and marshlands (Markó et al. 2004). It is a submissive species (Savolainen and Vepsäläinen 1989). It was studied in Romania in a mixed oak forest near Caluseri (two colonies), at the margin of a spruce forest in the Brețcu Mts. (two colonies), and on a mountain pasture in the Harghita Mts. (four colonies) in summer 2000.

Formica cinerea Mayr 1853 inhabits open, sandy areas (Czechowski et al. 2002). Some studies mention it among territorial species (Czechowski 1999, Seifert 2002), but other experiments prove its submissive character (Gallé 1991). It was studied on a sand dune complex near Tvärminne in S Finland (ten colonies) in summer 2002.

Formica balcanina Petrov & Collingwood 1993 was recently identified in Romania (Markó 1998). It occurs on open, arid areas from riverbanks to low mountain areas (Markó 1998). Its competitive state is not known, though on the basis of its lifestyle it is clearly non-territorial. Four colonies were studied at the margin of a vineyard at Caluseri, and four colonies near Bologa in summer 2001.

Lasius psammophilus Seifert 1992 is a common species in Europe inhabiting open sandy areas (Seifert 1992). On the basis of some studies (*L. alienus* in Gallé 1991, 1994) it is supposed to be an aggressive species, but submissive tendencies are known to occur in this species, as well (Czechowski et al. 2002). It was studied on a sand dune complex Tvärminne in S Finland (three nest-complexes) in summer 2002.

Spatial and temporal distribution of foragers around colonies

The most common method is baiting for the study of foraging success of ant species, as well as the properties of their communication system and competitive relationships (Gallé 1991, de Biseau et al. 1994, Gallé et al. 1994, Mody and Linsenmair 2003, Torres-Contreras and Vasquez 2004). Nevertheless the sole use of baiting experiments covers patterns occurring in the lack of such sources. Thus it is advisable to carry out observations both in the absence and in the presence of baits to get an accurate picture on the nature of foraging strategy and competitive status of a given ant species. Eight rectangular observation plots were established around the studied colonies (Fig. 1), and dynamics and the competitive behaviour of each ant species was recorded in the absence of baits on the first, and in the presence of baits on the following day. Observations were carried out from 8 A.M. to 9 P.M. Changes in climatic conditions as temperature of soil surface and relative air humidity above soil surface were recorded as well.

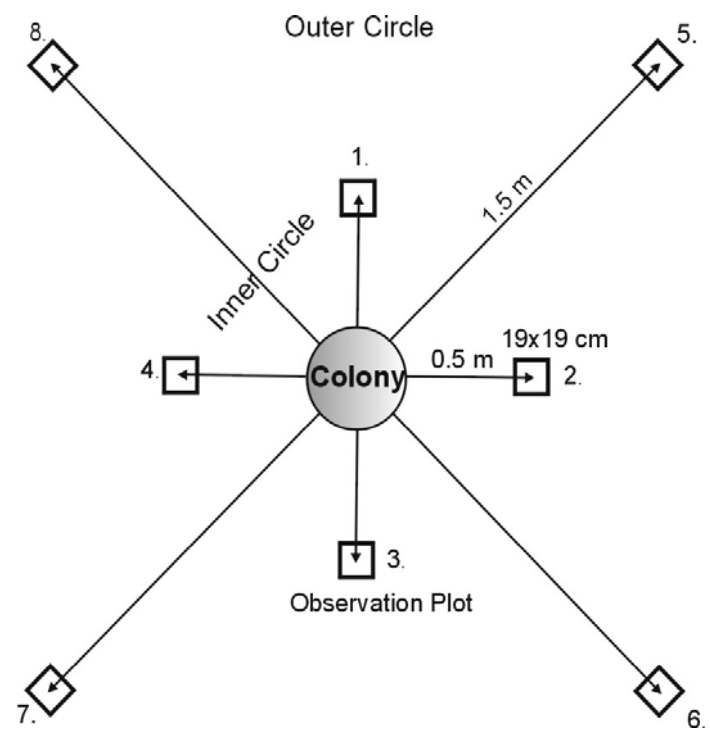


Fig. 1. The arrangement of observation plots around a colony.

SUMMARY OF NEW SCIENTIFIC RESULTS

1. Activity and climatic effects

The effect of climatic conditions on the activity of ants could be demonstrated mostly in species inhabiting open areas, as *L. psammophilus*, *F. balcanina*, and *F. cinerea*, and to a lesser extent in *M. ruginodis*. The different effect caused by the nature of habitat can be detected in *M. rubra*, where colonies living in open habitat are clearly influenced by changes in climatic factors as temperature and relative air humidity, whereas the same would not stand for colonies inhabiting forests. Differences in climatic preferences are at the base of peaceful coexistence in many ant species (Fernández-Escudero and Tinaut 1998, Orr et al. 2003), as in the case of *F. cinerea* and *L. psammophilus*.

2. The spatial distribution of discovery probability around colonies

The density of foragers of the studied species was higher close to their colonies in the majority of the cases, with the exception of *L. psammophilus*, where the minimum activity of the foragers underlined the accidental character of this species' foraging strategy, as well as its preference for the cooler periods of the day (e.g. evening, early morning). The observations suggest that individuals leave the immediate vicinity of the colony on diffuse exit paths, and thorough foraging activity begins only at a certain distance from a colony (Verron 1980, Dillier and Wehner 2004, Wehner et al. 2004).

3. The predictability of foraging success

The higher density of foragers in the immediate vicinity of colonies predicts the sooner discovery of food sources close to colonies, as well as the more enhanced exploitation of these sources. Although the majority of baits were discovered both by *F. cinerea* and *F. balcanina* still the exploitation pattern of baits was not as optimal as predicted. The clear priority of close sources could be detected solely in *M. rubra*. The foraging strategy of *M. ruginodis* seems to be slightly accidental, as close sources were not discovered in several cases, and preference of distant baits to discovered close baits was also observed. The extreme case, nevertheless, is represented by *L. psammophilus*.

4. Rivals

The presence of baits enhances the activity of ants significantly (Savolainen and Vepsäläinen 1988). The dominance of the studied ant species was sustained around their colonies in spite of the close neighbourhood of stronger species in some cases, as the case of *M. rubra* demonstrates in the vicinity of strong *F. rufa* colony. The case of *F. cinerea* vs. *F. rufa*, and *L. psammophilus* vs. *F. cinerea* also supports these observations. The negative effect of the dominant species could be detected in the *M. ruginodis* population at Lacul Dracului, where the presence of stronger *Manica rubida* significantly reduced the foraging activity of *M. ruginodis* in the presence of baits. A strange dualism appeared in *F. balcanina*, as well: whereas the dominance of this species was maintained in one population in front of *Tetramorium* sp. on baits, the dominance of *Tetramorium* sp. over *F. balcanina* occurred in another population in the presence of baits. The appearance of large ephemeral sources represented by baits causes the emergence of interspecific inhibition zones around the colonies of several species as *M. rubra*, and *F. cinerea*. The peaceful coexistence of *L. psammophilus* and *F. cinerea* is also ensured by spatial segregation despite of the close neighbourhood of their colonies.

5. Competitive success and position

Through the number and position of dominated food sources around their colonies it is possible to assess the success of different ant species in front of their competitors, as well as the frequency and outcome of interspecific conflicts. *M. rubra* won over aggressive species during our experiments, nevertheless it was considered to be a submissive species (Czechowski 1985, Savolainen and Vepsäläinen 1988, Vepsäläinen and Savolainen 1990), thus, on the basis of these results, it should be characterized as an aggressive species.

Different populations of the same species may display different competitive behaviour in *M. ruginodis*. This species was handled as submissive species up to now (Pisarski and Vepsäläinen 1989, Savolainen et al. 1989, Elmes 1991), but our results demonstrate a shift in its behaviour from aggressive to submissive status in the presence of a stronger competitor, e.g. *Manica rubida*.

Rival species rarely occur in the immediate vicinity of *F. cinerea* colonies, their distribution is mosaic-like. Contrary to the expectations species of lower competitive status can also win conflicts over *F. cinerea* when crowded on the baits (Markó and Czechowski 2004, Czechowski and Markó in press). *F. cinerea* is an aggressive species with territorial tendencies, but it can locally shift to submissive behaviour in the overwhelming presence of other species.

The behaviour of *L. psammophilus* is transitional from every point of view. Although conflicts with *F. cinerea* are mostly lost, it can also win when present in great numbers on sources. Its competitive behaviour is a mixture of aggressive and submissive behaviour (Markó and Czechowski 2004).

F. balcanina can also be characterized with high behavioural plasticity. Although it dominates in the absence of baits, the aggressive *Tetramorium* sp. (Czechowski 1979, Savolainen and Vepsäläinen 1988) can become dominant, when large sources appear even in the immediate vicinity of the *F. balcanina* colonies. The behaviour of *F. balcanina* is transitional: mostly aggressive in one of the studied populations, and shifting to submissive in the other population.

6. Optimization and self-organization

Complex colonial foraging patterns emerge from the interplay of simple individual behaviours (Pasteels et al. 1987a, b, de Biseau et al. 1994, Bonabeau et al. 1998, Mody and Linsenmair 2003, Röschard and Rocas 2003, Depickère et al. 2004). Our results support the presence of distance optimizing strategy only in *M. rubra*. *M. ruginodis* displays an entirely different strategy. Seemingly it is unexplainable why distant sources are exploited in this species when closer sources are also discovered. There are two possible explanations to this *a priori* suboptimal pattern (Detrain et al. 1999, Mody and Linsenmair 2003): (1) there is not enough available free forager to make possible the switching to the closer source through alternative recruitment; (2) in the event of high competitive pressure on close sources it pays to exploit even distant sources. The effect of competitive pressure on the foraging choices is supported in the case of *L. psammophilus*, as well. The high accuracy of the species' communication system allows this species to secure the source on short notice (Slaa et al. 2003). Competitive pressure determines the enhanced exploitation of distant sources in *F. balcanina*, too. The species' deficient recruitment strategy constitutes a major handicap when competing for food with the much more effectively recruiting *Tetramorium* sp.

The majority of baits are discovered by *F. cinerea* around its colonies, still distant sources are preferred in some cases. Its colonies were large and the competitive pressure

was low, even at colonies surrounded by *F. rufa* nests. The suboptimal foraging pattern can be explained in two ways: (1) the exploited distant baits were close to active trunk trails; (2) the distant bait was first discovered by larger number of foragers, which ensured a higher recruitment rate to this source and the preference stabilized later.

7. Task partitioning in *F. cinerea*

The baiting experiments carried out around *F. cinerea* colonies reveal an unknown character of the species' foraging strategy. The presence of trunk trails obviously raises the question whether task partitioning between foragers occurs (Anderson and Ratnieks 2000). The results convincingly prove that trunk trail foragers are conservative, and the activity on trails is not influenced by the presence of large ephemeral sources on the sand surface. The stability of trunk trail activity makes possible the continuous exploitation of stable sources like aphid colonies, and also secures the colony's 'possession' (Grasso et al. 1998, Mody and Linsenmair 2003).

What is then the optimum? It seems that the optimality of a decision, of a pattern, of a strategy cannot be understood without considering the proper ecological context. The analysis of competitive relationships helps us improve understanding the foraging strategies and their plasticity in ants, especially in non-territorial species. The behaviour of non-territorial ants does not necessarily matches rigid categories. Their plastic behaviour ensures their survival in dominant and subdominant position, as well. The plasticity of individual behaviour, and even the suboptimality of an individual choice can cause the emergence of optimal patterns on colony level (Pasteels et al. 1987a, b, Savolainen 1991, Schatz et al. 1999).

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