The foraging strategy of *Formica sanguinea* (Hymenoptera: Formicidae), a facultative slave-maker

Piotr Ślipiński, Bálint Markó, Tomasz Włodarczyk & Wojciech Czechowski

Abstract

There are almost no hard data on the competitive status of *Formica sanguinea*, and previous studies focus mainly on its spectacular lifestyle as a slave-maker. It is usually described as an aggressive and territorial species, the latter due to its raiding behaviour and morphological resemblance to species of the subgenus *Formica* s. str. (typical territorial species and top dominants). A series of field observations using baits was carried out across the longitudinal extent of *F. sanguinea*’s range in Europe, from Finland through Poland to Romania. The main objective of the present study was to determine the competitive abilities of *F. sanguinea* and its status in the interspecific ant hierarchy. We also investigated the changes in the competitive abilities of *F. sanguinea* along the meridional axis of the species’ range. Based on our results, the distribution of *F. sanguinea* foragers around the nest showed a distance dependent pattern, with fewer individuals present in distant areas and at distant baits. While in the absence of baits, other ant species were seemingly not influenced by the abundance of *F. sanguinea*, this changed in the presence of baits, showing that *F. sanguinea* has a negative effect on other species. Still, many baits were exploited by other ant species around the studied nests. There were also clear differences among the study regions in terms of bait utilisation, with Finnish colonies exploiting most of baits, while Romanian colonies mostly neglecting them. In light of the present study and due to the complexity of the competitive strategy of the species, we believe that *F. sanguinea* does not fall into the conventionally arranged three-level hierarchy of interspecific ant competition. In addition, *F. sanguinea*’s competitive ability may depend on local ecological conditions as revealed by the comparison of different populations across Europe.

Key words: Competition, dominance hierarchy, subordinate species, territoriality.

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Introduction

Competition is a widely studied interaction of animals, also specifically of ants. Although its primary importance in structuring ecological assemblages has long been disputed, it is generally (with exceptions, e.g., Gish & Johansson 2011) accepted that it plays a significant role for ants at least in the temperate climate (e.g., Reznikova 1983, Savolainen & Vepsäläinen 1988, Savolainen & al. 1989, Sanders & Gordon 2003, Adler & al. 2007, Cerda & al. 2013, Retana & al. 2015). Ants are easy targets for studying the role of competition, since they can be found in high abundance in a wide variety of terrestrial habitats. Competition among ants is studied on many ecological levels, starting from the direct interactions between individuals and colonies (e.g., Czechowski 1999, 2004, Markó & Czechowski 2004, Czechowski & Markó 2005, Czechowski & al. 2009, Maák & al. 2014, Vepsäläinen & Czechowski 2014, Ślipiński & Żmihorski 2017) to the role of competition in the formation of multispecies ant assemblages (e.g., Savolainen & Vepsäläinen 1989, Väänänen & al. 2010, Czechowski & al. 2013, Markó & al. 2013, Ślipiński & al. 2014, Trigos Peral & al. 2016, Żmihorski & Ślipiński 2016; for a review, see Adams 2016).

The evolutionary effect of competition within ant assemblages manifests itself in the differentiation of foraging strategies by the spatial and/or temporal separation of ecological niches (both in terms of food and habitat). Based on competitive status, ant assemblages in the temperate zone (but not only, see Cerda & al. 1997, 2013) are organized hierarchically according to the concept outlined by Reznikova (1980, 1983) and developed by Pisarski & Vepsäläinen (see Vepsäläinen & Pisarski 1982, Savolainen & Vepsäläinen 1988, Pisarski & Vepsäläinen 1989). The top level consists of aggressive territorial species, whose colonies defend their whole foraging areas against other territorial species, and limit the nesting and foraging possibilities of subordinate species within them. The intermediate level includes aggressive non-territorial species (encounterers) able to defend individual food resources. The lowest level
is made up of the least aggressive species, submissive to all stronger competitors. It is also important to mention that in some habitats, species may not be arranged in dominance hierarchies, or if they are, those dominance hierarchies are very context dependent (Stible & al. 2017).

Unless previous data offer reliable clues, it is hard to assess a priori which species could be the dominant ones under natural conditions. Usually, the level of aggression displayed by an ant species towards others is thought to be a good predictor about the position of one in relation to the other. A good example are wood ants of the Formica rufa group – common top dominants of ant assemblages in the Euro-Siberian forests, which are known to engage in territorial disputes, frequently linked to predation as well (de Bruyn & Mabelis 1972, Mabelis 1979, Drieden & al. 1984, Punttila & al. 1996, Domisch & al. 2005). However, there is another group of ants known to behave quite aggressively towards others: slave-making ants. Slave-makers, facilitative or obligate ones, raid nests of the so-called slave species and take the brood while killing and/or driving away the slaves. (D’Ettorre & Heinze 2001). The level of aggression is so high here that one could assume that slave-maker species, at least those with big workers and large-sized colonies, like the amazon ants (Polyergus spp.) and blood-red ants (subgenus Raptiformica), should dominate in their assemblages (Wittman & Gotelli 2011). However, there are almost no direct observations of the competitiveness of these ant species, since the focus is mostly set on various aspects of their spectacular socially parasitic lifestyle (e.g., Buschinger & al. 1980, Czechowski & Rotkiewicz 1996, Sandoinen & Deslauriers 1996, D’Ettorre & Heinze 2001, Mori & al. 2001, Kaspary & Trager 2007, Apple & al. 2014).

The facultative slave-maker blood-red ant, Formica (Raptiformica) sanguinea, is a common Palaearctic species (Czechowski & al. 2012). Typically, it enslaves ants of the subgenus Serviformica. As a rule, the slaves (if any) are a minority of the colony (see Czechowski 1996), and perform mainly intra-nest tasks (Kharik 1997a, b). Therefore, F. sanguinea is assumed to engage in day to day interactions with other ant colonies in its vicinity, unlike the obligate slave-maker Polyergus spp., which do this through their slaves (Mori & al. 2001). In the current literature, F. sanguinea is mainly classified as an aggressive territorial species (Vepsäläinen & Peisker 1982, Sandoinen & al. 1989, Punttila & al. 1996, Czechowski 2000, Czechowski & Marko 2006, Väänänen & al. 2010). Czechowski (2000) described it as a territorial species that does not respect the boundaries of foreign territories during its raiding periods. Formica sanguinea’s supposed dominant competitive status is supported by its high aggressiveness, raiding behaviour, and morphological resemblance to territorial wood ant species, with no specific data supporting this.

The main objective of the present field study was to fill this gap in the knowledge about Formica sanguinea’s competitive ability and to determine its status in the inter-specific ant hierarchy based on standard field observations of foraging behaviour with the use of baits placed around colonies. We proposed to characterize F. sanguinea’s relationship with other species based on changes in the abundance of its workers and the workers of other ant species recorded around F. sanguinea nests, as well as by using the exploitation success of artificial food sources as a proxy for its competitive dominance.

In particular, we tried to answer three main questions. (1) Does Formica sanguinea exert a strong competitive pressure on other ant species? To answer this question we recorded the abundance of F. sanguinea and other ant species around their nests, and also analysed the distance-related food source exploitation pattern. (2) Do the competitive abilities of F. sanguinea change along the meridional axis of the species’ range, i.e., under different environmental conditions? Bait discovery and occupancy ratio was used as a proxy for the competitive success of Finnish, Polish and Romanian populations. (3) Do slaves make a noticeable contribution to the competitive success of F. sanguinea? By measuring the foraging activity of F. fusca slaves at baits and their relation to the activity of F. sanguinea workers, we tried to estimate the effect of slaves on the competitive abilities of the colonies.

Methods

Study sites: We carried out the field work in 2007–2009 in southern Finland, Poland and Romania. The study sites were situated approximately along the longitudinal extent of the Formica sanguinea range in Europe, forming a transect of about 1500 km (Fig. 1). The northern part of the range (Finland) was in the cold temperate climate zone, while the central (Poland) and southern (Romania) parts (also a considerable distance from each other) were in the warm temperate climate zone.

The Finnish study site was located near the village of Tännäiska (59° 50’ N, 23° 15’ E) on the Hanko Peninsula. The site was a complex of sand dunes surrounded by a mature Scots pine (Pinus sylvestris) dry forest. The sandy soil was covered mostly by patches of moss and lichens, and locally with patches of grass. For the detailed habitat characteristics of the area, see e.g., Palmgren (1972) and Gallè (1991). The field work was carried out in 2008 and 2009. Two colonies of Formica sanguinea (FI and FII), each nesting in the open sandy area close to the forest margin, were studied each year in July.

There were two study sites in Poland: near the city of Białystok (53°14’ N, 23°16’ E) in the Podlasie Lowland and in the town of Otwock (52°09’ N, 21°16’ E) in the Mazovian Lowland. Both sites were located within moist mixed pine forests of Scots pine, pedunculate oak (Quercus robur) and silver birch (Betula pendula) trees, with junipers (Juniperus), alder buckthorns (Frangula alnus) and rowans (Sorbus aucuparia) in the undergrowth. The field work was carried out in 2008–2009. A total of five colonies of Formica sanguinea were studied: two near Otwock (PI and PII) and
three (PII - PV) near Białystok, in the summers of 2008 (PI, PII, PIII) and 2009 (PII, PIV, PV). Additionally, some of the colonies were also studied in the autumns of 2008 (PI) and 2009 (PIII, PIV, PV). All of the colonies were located at the edge of a forest or in forest clearings.

In Romania, the study site was located in the southern part of the Giurgeului depression (46° 36' N; 25° 36' E; 780 m a.s.l.) in the eastern Carpathians, Transylvania. The site was a vast semi-moist meadow of the Molinion caeruleae alliance (with, among others, Molinia caerulea, Deschampsia cespitosa, Festuca pratensis, Nardus stricta and Juncus sp.), densely overgrown with small birch saplings. The meadow was fairly intensely grazed by cows for most of the year. This is also the location of the largest known European polydomous system of Formica exsecta (Markó & al. 2012). The field work was carried out in 2007 - 2009. Five F. sanguinea colonies (RI - RV) were studied in the summers of 2007 (RI, RII), 2008 (RII, RIV), 2009 (RV). All colonies were situated at the edge of the meadow, beyond the range of F. exsecta.

All Polish colonies contained Formica fusca slaves. Colonies in Finland and Romania seemed to have no slaves; at least their activity outside the nests was not noticeable at all. Individual workers of potential slave species, such as F. rufibarbis, foraged in very small numbers around F. sanguinea nests in Romania; however, they were not slaves. All species in the study were identified according to the key provided by CzeChowski & al. (2012).

**Field observations:** Baits were used to study the foraging patterns and behaviour of ants around their nests. The presence of large food sources enhances, and thus alters, the activity of ants in the specific area where the bait is placed (Vepsäläinen & Piasecki 1982, Savolainen & Vepsäläinen 1988, Vepsäläinen & Savolainen 1990). For this reason, the distribution and abundance of foragers should be recorded before the baits are placed (control observations) to obtain an appropriate view of the foraging strategy of a specific ant species (see Markó & CzeChowski 2004, CzeChowski & Markó 2005, Góbi & Párr 2010, Petráková & Schlagamerksky 2011, Markó & CzeChowski 2012, CzeChowski & al. 2013, Markó & al. 2013).

We established eight rectangular (19 cm × 19 cm) observation arenas around the nest areas of the studied Formica sanguinea colonies; “nest area” is defined as an area covered with nest entrances. The arenas were arranged in two distance categories (inner and outer zone), with each category containing four arenas. The centres of the inner zone arenas were at a distance of 0.5 m from the border of the colony’s nest area, while the centres of the outer zone arenas were at a distance of 1.5 m (Fig. 2). When studying the foraging of ants in laboratory experiments, much smaller distances are generally applied between an ant nest and the food source (see e.g., de Biseau & al. 1997, de Biseau & Pasteels 2000). Thus, we considered that the distances applied in our research could offer reliable information on the distribution of foragers around the colonies in the field.

The location of the first arena (no. 1) was arranged toward the North, with the subsequent arenas following it at a regular distance in a clockwise direction (see also Markó & CzeChowski 2004, CzeChowski & Markó 2005, Markó & CzeChowski 2012; Fig. 2).

Each colony was observed for two days: the first day observations were made in the absence of baits (control), whereas on the second day, baits were put out in the centre of each arena. To avoid any effect due to the seasonal variation in food preferences, baits contained both animal protein (tuna flakes) and carbohydrate (mixed-flower honey) in a 2:1 proportion. Bait portions of ca 3.5 cm in diameter were placed on 9.5 cm plastic plates. The portions were put out 30 min. before the first observation at the beginning of each period. Observations were carried out during two periods of a day (09:00 - 12:00, 17:00 - 20:00), covering the activity peaks of the ants. During each period, each arena was checked for one minute every 20 minutes (N = 18 observations). The number and species/genus identity of the foraging ants were recorded in the arena and at the bait, respectively. Information about the number of individuals foraging in a restricted space (arena) in a specific time period (one minute) gave us the basic variables used in the statistical models for abundance. The baits were retrieved at the end of each observation period.

**Data analysis:** Generalized Linear Mixed Models (GLMM, negative binomial, maximum likelihood fit) were used to test the effect of distance (inner vs outer observation zone) from the nest border on the abundance of Formica sanguinea workers around their nests, both in the absence and presence of baits. Observation zone (inner vs outer) and region (Finland, Poland, Romania) were included as fixed factors, whereas year, season and observation time were the nested random factors, in addition to colony ID and arena ID, in order to handle dependencies. The analyses were carried out separately for both control and bait observations. All observations were considered in both analyses (N = 2880).

A similar approach (GLMM, Poisson distribution, maximum likelihood fit) was used to analyse the occurrence of ants of other species foraging around Formica sanguinea colonies in the absence and presence of baits. In addition to observation zone and region, the number of F. sanguinea workers was also included as a covariate to test if there was a negative effect of F. sanguinea abundance on the abundance of workers of subordinate species. The same random...
factors were applied as previously. All observations were considered in both analyses (N = 2880).

The distribution of *Formica fusca* slave individuals around *F. sanguinea* nests in Poland (N = 1584) was analysed also with the GLMM (Poisson distribution, maximum likelihood fit). There were no slaves observed around *F. sanguinea* colonies in Finland and Romania. Observation zone (inner vs outer) and number of *F. sanguinea* workers was included in the models as well as their interaction, in order to see whether the relationship between slaves and *F. sanguinea*’s abundance is distance related. The random factors remained the same as in the previous models. The analyses were carried out for both the control and bait observations.

We used the Czekanowski index to calculate whether there is high or low niche overlap between *Formica sanguinea* and other (subordinate) ant species foraging around *F. sanguinea* colonies in the absence and presence of baits in two observation zones (inner vs outer). This is a symmetrical index that ranges from 0 (no overlap) to 1 (complete overlap). The analysis reveals whether the average niche overlap is more or less than would be expected if the species used the resource independently of one another. The average pairwise niche overlap was then compared to the average calculated for the randomized assemblages. Communities were randomized 5000 times using the randomization algorithm 2 (RA2) of the niche overlap model (WITTMAN & al. 2010, GOTTLEI & al. 2015).

To estimate the food utilization efficiency of *Formica sanguinea* workers, we compared the number of baits discovered to those exploited by *F. sanguinea* with the χ²-test. A bait was considered discovered if at least one *F. sanguinea* worker was observed at it. We considered a bait as exploited when the average number of workers at a bait reached at least one per day. The same approach was used to estimate the food utilization efficiency of ants of other species foraging around *F. sanguinea* colonies.

All statistical analyses were carried out in the R Statistical Environment (R CO RE TEAM 2016) with α = 0.05 significance level. All GLMMs were performed using the glmer and glmernb functions in the lme4 package (BATES & al. 2014). The Glht function was used in the multcomp package in order to carry out post-hoc sequential com-

Fig. 3: The relationship between the abundance of *Formica sanguinea* workers and workers of subordinate species (mean values in the 95% confidence interval) and the distance from the nest area border (inner and outer zone; at the top), and region (at the bottom) in the absence and in the presence of baits.
parisons with Tukey contrasts among the multiple factor levels when performing the GLMMs (Hothorn et al. 2008). Czernakowski index was calculated with the help of EcoSimR package (Gotelli et al. 2015).

Results

Influence of the distance from the nest and the geographic region on the abundance of *F. sanguinea*: According to the GLMM results, the abundance of *Formica sanguinea* workers in the control phase was related to the distance from the nest border ($\chi^2 = 30.7$, $p < 0.001$): there were significantly fewer workers in the outer zone than in the inner zone (GLMM $z = -5.54$, $p < 0.001$; Fig. 3, Tab. 1). There were significant differences in the abundance of *F. sanguinea* among regions as well ($\chi^2 = 8.08$, $p = 0.017$): the abundance of *F. sanguinea* was significantly lower in Romanian colonies than in the Finnish ones ($z = -2.84$, $p = 0.01$), but there were no differences in the other comparisons ($z \geq -1.71$, $p > 0.26$; Fig. 3).

Similarly to the control situation, the abundance of *F. sanguinea* workers was related to the distance from the nest border at baits as well ($\chi^2 = 4.67$, $p = 0.03$): their abundance was lower at the baits of the outer zone (GLMM $z = -2.16$, $p < 0.03$; Fig. 3, Tab. 1). There were differences among the regions as well ($\chi^2 = 76.84$, $p < 0.001$): significantly more *F. sanguinea* foragers were present at baits in Finland, than in Poland ($z = -7.52$, $p < 0.001$) and Romania ($z = -6.84$, $p < 0.001$), but there was no significant difference between Polish and Romanian *F. sanguinea* colonies in this respect ($z = -2$, $p = 0.14$; Fig. 3).

Efficiency of food resource utilization by *F. sanguinea* and subordinate species: *Formica sanguinea* workers discovered a total of 72% of all baits, but exploited only a fraction of them (31.8%), and this inefficiency was especially noticeable in the Romanian colonies (Tab. 2). The number of baits discovered and exploited significantly differed among the regions (Finland vs Poland $\chi^2 = 3.96$, $df = 1$, $p < 0.004$, Finland vs Romania $\chi^2 = 11.96$, $df = 1$, $p < 0.001$, Poland vs Romania $\chi^2 = 5.06$, $df = 1$, $p < 0.04$). Subordinate workers were recorded on most baits (62-78%) placed around *F. sanguinea* colonies; they exploited a considerable percentage of baits in Finland (37%) and Poland (42%), but only 12.5% in Romania.

The activity of subordinate species around *F. sanguinea* nests: Altogether, we recorded subordinate (non-territorial) species of six ant genera within the arenas and at baits around the investigated *Formica sanguinea* nests: *Myrmica, Leptothorax, Temnothorax, Tetramorium, Formica* (subgenus *Serviformica*) and *Lasius* s. str. In Finland, workers of *Myrmica sp.*, *Temnothorax sp.*, *Tetramorium cf. caespitum* and *Lasius psammophilus* were recorded. In Poland, only those of *M. ruginodis, Leptothorax acervorum* and *T. cf. caespitum*, while individuals of *Myrmica sp.*, *L. acervorum* and *Lasius platy thorax* as well as those of *F. rufiharbis* were observed in Romania.

The abundance of these ant species was not related to the abundance of *Formica sanguinea* in the absence of baits (control) (GLMM $\chi^2 = 0.48$, $z = -0.69$, $p = 0.48$; see Tab. 1), and there were no differences in their abundance between the two observation zones ($\chi^2 = -0.32$, $z = -0.57$, $p = 0.56$), and among different geographical regions ($\chi^2 = 0.77$, $z < 0.86$, $p > 0.38$; Fig. 3).

At baits, however, the abundance of subordinate ant species was negatively related to the abundance of *Formica sanguinea* (GLMM $\chi^2 = 259.34$, $z = -16.1$, $p < 0.001$). There was also a significant difference in their distribution between the inner and outer zones ($\chi^2 = 6.58$, $p = 0.01$), as there were more ants present at distant baits ($z = 2.56$, $p = 0.01$). No

Tab. 1: Detailed results of the various GLMM analyses.

<table>
<thead>
<tr>
<th>Output variable</th>
<th>Input variables and factors</th>
<th>Model outputs</th>
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<tr>
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<td>Standard error</td>
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<td>Region (Poland vs. Romania)</td>
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<tr>
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<td>Region (Finland vs. Poland)</td>
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<td>Abundance of subordinate species – bait</td>
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significant differences were registered among the regions ($\chi^2 = 1.06, \text{ } z > -0.87, p = 0.38; \text{ } \text{Fig. 3})$.

The temporal niche overlap index calculated for Formica sanguinea and subordinate ant species foraging around $F. \text{ sanguinea}$ colonies (0.06) did not significantly differ (SES $-1.85$, non-significant tail probabilities falling between $-2.0$ and $+2.0$) from the expected value (0.07) in the control phase, indicating that there was no spatio-temporal segregation between species in the absence of food sources. However, in the presence of baits, the calculated index (0.04) was significantly smaller (SES $-17.46$) than the expected one (0.16), revealing significant spatio-temporal segregation between $F. \text{ sanguinea}$ and subordinate ant species.

The foraging activity of slaves in $F. \text{ sanguinea}$ colonies: The abundance of Formica sanguinea workers was related to the abundance of $F. \text{ fusca}$ slaves (Fig. 4) both in the absence and in the presence of baits ($z = 3.44, p = 0.00; \text{ } z = 3.56, p = 0.00$, respectively; see Tab. 1). In the presence of these baits, the relationship between $F. \text{ sanguinea}$'s abundance and the abundance of slaves was stronger within the inner zone than in the outer zone ($z = -2.39, p = 0.01$). No significant differences were registered in the abundance of $F. \text{ fusca}$ slave workers between the two observation zones in the absence of baits ($z = -0.02, p = 0.98$).

Discussion

One of the main objectives of the study was to determine the competitive ability of Formica sanguinea in relation to co-occurring non-territorial ant species. Originally, it could be presumed that if $F. \text{ sanguinea}$ is a truly strong competitor, the presence of its workers should have a negative impact on the presence of workers of the subordinate species within the shared parts of the foraging area. This inhibitive effect should be especially evident during competition for food resources (see PIESARSKI & VEPSÄLÄINEN 1989, CERRA & al. 2013). However, the results generally indicate the very plastic and variable competitive abilities of $F. \text{ sanguinea}$ during periods of their routine foraging activity (i.e., outside their raiding activity). In general, workers of $F. \text{ sanguinea}$ exert some pressure on foragers of the other species, however, their negative impact on the activity of the latter was mostly visible only in the presence of baits and was very limited spatially. Possible competitors of $F. \text{ sanguinea}$ are allowed to forage casually in the common area. In no case is this a strategy typical of territorial species, which would significantly reduce the foraging activity of subordinates (both submissives and encounters) within their territories. Even at baits, the negative influence of $F. \text{ sanguinea}$ on foragers of co-occurring species is very short-range, practically restricted to the baits closest to the nest. More distant baits can be more or less freely utilized by other ants even though such a distance, i.e., 1.5 m from the borders of the nest area, can easily be covered by $F. \text{ sanguinea}$ workers (their raiding columns are able to reach target colonies at 100 m distance in one way; CZECHOWSKI & RADCHENKO 2006). Moreover, in some cases, $F. \text{ sanguinea}$ does not even exploit all the baits close to its nest. In typical territorial species (e.g., Formica polycletana, F. exsecta, Lasius fuliginosus), the negative impact on the foraging activity of subordinate species, not to mention the use of baits as such, is incomparably more spectacular than that shown here for $F. \text{ sanguinea}$ (see e.g., SALOAINEN & VEPSÄLÄINEN 1988, VEPSÄLÄINEN & SALOAINEN 1990, CZECHOWSKI & MARKÓ 2006, CZECHOWSKI & al. 2013, MARKÓ & al. 2013, TRIGOS PERAL & al. 2016).

Our study revealed the variance in the efficiency of food source exploitation in different regions and habitats, which indicates that Formica sanguinea's competitive abilities are not fixed and may depend on local ecological conditions. In the north (Finland), $F. \text{ sanguinea}$ was definitely the dominant species in terms of the monopolization of food sources (baits). The farther to the south (Poland, and especially Romania), the more ground it gave to other ants (Fig. 3). At the southern end of the gradient (Romania), $F. \text{ sanguinea}$'s interest in the baits was scant, even in the direct vicinity of its nests, and the baits were definitely dominated by foragers of the subordinate species. The results suggest a gradual decrease in the competitiveness of $F. \text{ sanguinea}$ from the north to the south along the meridional extent of its range; however, there are only four sites in the study, so the power to detect a latitudinal effect is low. This variation may be caused by climatic conditions linked to differences in the geographical locations of $F. \text{ sanguinea}$ colonies, such as the length of the vegetation period, mean temperatures, etc. It is known that ants living in the north must work especially intensively to provide offspring with enough protein food, essential for development in conditions of a shortened vegetation period (PUNITILA & al. 2004). An undoubted consequence of this is an increasing intensity of interspecific competition.

The other question studied was the possible contribution of slaves to the foraging strategy of Formica sanguinea. The significance of slaves for the fitness and competitiveness of mixed colonies depends first of all on the nature of the relationship between the social parasite and its host species (see BUSCHINGER & al. 1980, MORI & al. 2000, 2001). Obligate slave-makers are usually morphologically and behaviourally adapted and specialized in acquiring slaves (MORI & al. 2001, BUSCHINGER 2009, D’ETTORE & HEINZE 2001). In their colonies, slave-maker workers are often significantly outnumbered by slaves (e.g., MARKOVSKY 1974, COOL-KWAIT & TOPP 1984, MORI & al. 2001), which fulfil all daily tasks, including foraging. As a result, the slave species determines

### Tab. 2: Bait discovery and exploitation (%) by Formica sanguinea and subordinate species around the investigated nests

<table>
<thead>
<tr>
<th>Country</th>
<th>Bait discovery / exploitation (%)</th>
<th>Subordinate species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Finland</td>
<td>100.00 / 84.37</td>
<td>78.00 / 37.00</td>
</tr>
<tr>
<td>Poland</td>
<td>67.00 / 26.13</td>
<td>69.00 / 42.00</td>
</tr>
<tr>
<td>Romania</td>
<td>60.00 / 2.50</td>
<td>62.00 / 12.50</td>
</tr>
</tbody>
</table>

### Fig. 4: The relationship between the abundance of Formica sanguinea workers and $F. \text{ fusca}$ slaves (mean values in the 95% confidence interval) and the distance.
the competitive ability of the obligate slave-maker colony and its relations with neighbours (Buschinger 2009). A different situation is found in the colonies of facultative slave-makers, like F. sanguinea and other species of the subgenus Rapiformica, where the proportion of slaves (if any) is typically much smaller. It usually does not exceed a few percent (Czechowski 1996, Buschinger 2009, D’Ettore & Heinze 2001), and possessing slaves is a kind of “luxury” for these ants. Therefore, the impact of slaves on colony fitness (see Savolainen & Deslippe 1996) and competitiveness must be much smaller in this case, though it should not be ignored. Slaves may have indirect and direct influence. Indirect, because the presence of slaves, which usually perform intrandial tasks (Kharkiv 1997a, b) allows the colony to designate higher numbers of F. sanguinea workers (more aggressive and physically stronger than their typical slaves from the Serviformica subgenus) to tasks outside the nest. Direct, because some of the slaves, especially if there are enough of them, participate in foraging and may enrich in some way the foraging strategy of F. sanguinea with their own contribution, such as, e.g., opportunism, which is characteristic for F. fusca or F. cunicularia. On the other hand, quite aggressive slave species also exist, such as F. rufibarbis or F. cinerea (the latter even with an inclination toward territoriality; Czechowski & Markó 2005) or, in exceptional cases, even typically territorial species of the subgenera Coptoformica and Formica s. str., which occasionally occur as slaves in F. sanguinea colonies (Czechowski 1996).

A positive relationship was found between the activity of Formica sanguinea workers and F. fusca in the F. sanguinea colonies studied here. The abundance of F. sanguinea workers positively influenced the abundance of F. fusca slaves. From the above, one can conclude that the foraging activity of slaves increases the competitive ability of F. sanguinea colonies to a certain extent, especially when slaves (as in this case) forage for food. In this context, it is worth mentioning the tendency of slaves, even of such submissive species as F. fusca, to accompany F. sanguinea during slave raids, which are meant also as a form of foraging (Dobrzanski 1965, Mori & al. 2001). They can even directly participate in robbing pupae (Dobrzanski 1961, Czechowski 1977, 1998).

The foraging strategy of Formica sanguinea and its competitive abilities cannot be considered separately from the slave raids as a possible mechanism of both foraging and competition. Darwin (1859) had already derived that ant slavery ensues from myrmecophagy. Today, predation on other ants, and also robbing foreign broods — by itself or in connection with other factors — is considered to be the origin of slavery in ants (e.g., Buschinger 1990, 2009, Hölldobler & Wilson 1990). According to Dobrzanki’s (1965) theory, slave raids are a form of foraging in the case of F. sanguinea, and the route of a raid is a peculiarly “elongated foraging area”. It is a fact that most of the spoils of raids are consumed in F. sanguinea colonies (Dobrzanski 1965, Mori & al. 2001). The large larvae and pupae of slave species’ sexuals, which F. sanguinea (unlike Polyergus) robs equally along with those of the workers, must all be used as food. Besides their immediate trophic importance, slave raids by their very nature are a mechanism of long-term competitive pressure on nearby colonies of the slave species due to the systematic weakening of their populations. Moreover, the clearly predatory-competitive F. sanguinea raids are also known to occur against colonies of both slave- and non-slave subordinate species (Czechowski 1977, 2004; see below). This means that a colony of F. sanguinea can control colonies of other ants within the range of its raiding columns, i.e., a radius of dozens of metres from its own nest (see, e.g., Dobrzanski 1961, Buschinger & al. 1980, Mori & al. 2000, D’Ettore & Heinze 2001, Czechowski & Radchenko 2006), periodically decreasing their competitive abilities. In this context, especially spectacular was an event observed on the sand dunes in Finland (!) in 1998. After years of co-existence, a local F. sanguinea colony suddenly, as the result of a four-day raid (4–7 July), totally annihilated a dense polydomous system of F. cinerea within an area of ca 500 m² (successional Stage 5 in Gallé 1991; see also Czechowski & al. 2005) and settled permanently there, taking over F. cinerea nests. During these extremely fierce attacks, F. sanguinea massacred F. cinerea workers, chasing them even on grass blades; corpses, in large numbers, were taken to the F. sanguinea nest (W. Czechowski, unpubl.). This observation illustrates well Seiffert’s (1987) statement that at an initial stage of population development, F. sanguinea exploits Serviformica species as the hosts of its social parasitism, but later, as their populations develop and colonies are ready to spread by splitting, it tends to erode the competing slave species within its range. At the same time, the observation, compared with those on the purely (if such really exist) socially parasitic relationship between F. sanguinea and F. cinerea (see Czechowski & Rotkiewicz 1996), is one more argument for the circumstance-dependent variability of the life strategy of F. sanguinea.

Based on the results of this study and general knowledge on the biology of the species, two spheres of activity of Formica sanguinea together comprise the competitive abilities of this species: (1) the sphere studied here — the everyday routine, around-nest foraging supported by a share of the slaves, with generally moderate but flexible (according to local conditions) pressure on neighbouring foreign ants, and (2) the periodical raiding of slave and non-slave species, radically weakening their competitive abilities. Therefore, the words which seem to most correctly characterize the competitive strategy of F. sanguinea are “plasticity” and “complexity”.

As was stated in the introduction, Formica sanguinea has thus far been commonly assumed to be a territorial species. In light of the present study, and due to the complexity of its competitive strategy, the species does not fall into the conventionally arranged three-level interspecific ant competition hierarchy (see, e.g., Pisarski & Vepsäläinen 1989). To vividly emphasize the unique nature of F. sanguinea in this respect — by updating a former expression (Czechowski 2000) — it can be described as a non-territorial ant species which, during its slave raids, does not respect the boundaries of territorial species.

The results of this study are particularly interesting in light of the recent review of Stubbe & al. (2017), in which the authors encourage scientists to shake off the confines of thinking about species as being arranged in transitive hierarchies and to consider ant communities as networks of interacting species, rather than linear hierarchies in which they can easily be ranked from most to least dominant. And also to “compare the organization of communities across sites, habitats, climates”, as it was performed within the framework of the present study. We hope that our study will be one more step in developing the discussion about the interspecific competitive relationships of ants.
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