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## 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 arenas 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., GIBB & 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, CERDÁ & 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, MAAK & 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 CERDÁ & 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 (STUBLE & 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, DRIESSEN & 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, facultative or obligate ones, raid nests of the so-called slave species and take the brood while killing and/or driving away the defenders (DOBRAŃSKI 1961, MORI & al. 2001, BUSCHINGER 2009, D'ETTORE & 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, SAVOLAINEN & DESLIPPE 1996, D'ETTORE & HEINZE 2001, MORI & al. 2001, KING & 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 (KHARKIV 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 & PISARSKI 1982, SAVOLAINEN & al. 1989, PUNTTILA & al. 1996, CZECHOWSKI 2000, CZECHOWSKI & MARKÓ 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.

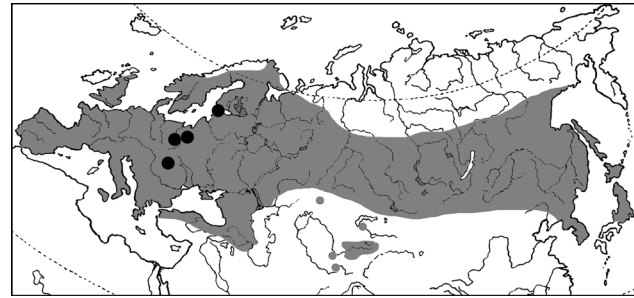


Fig. 1: Location of study sites (black dots) on the distribution map of *Formica sanguinea* in the Palaearctic (based on CZECHOWSKI & al. 2012).

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 Tvärminne (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 GALLÉ (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° 6' 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 (PIII - PV) near Białystok, in the summers of 2008 (PI, PII, PIII) and 2009 (PI, PIV, PV). Additionally, some of the colonies were also studied in the autumns of 2008 (PI) and 2009 (PII, 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 & PISARSKI 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, GIBB & PARR 2010, PETRÁKOVÁ & SCHLAGHAMERSKÝ 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 cen-

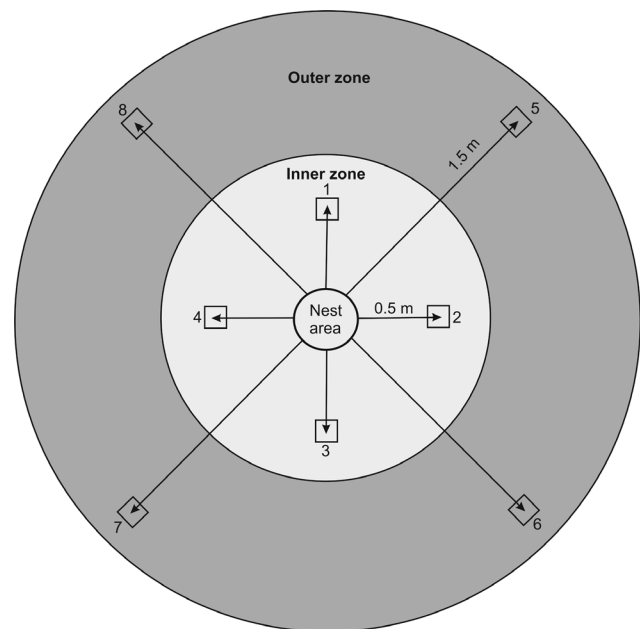


Fig. 2: Arrangement of the observation arenas (1 - 8) within two zones (inner and outer) around the *Formica sanguinea* nest area.

tre 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

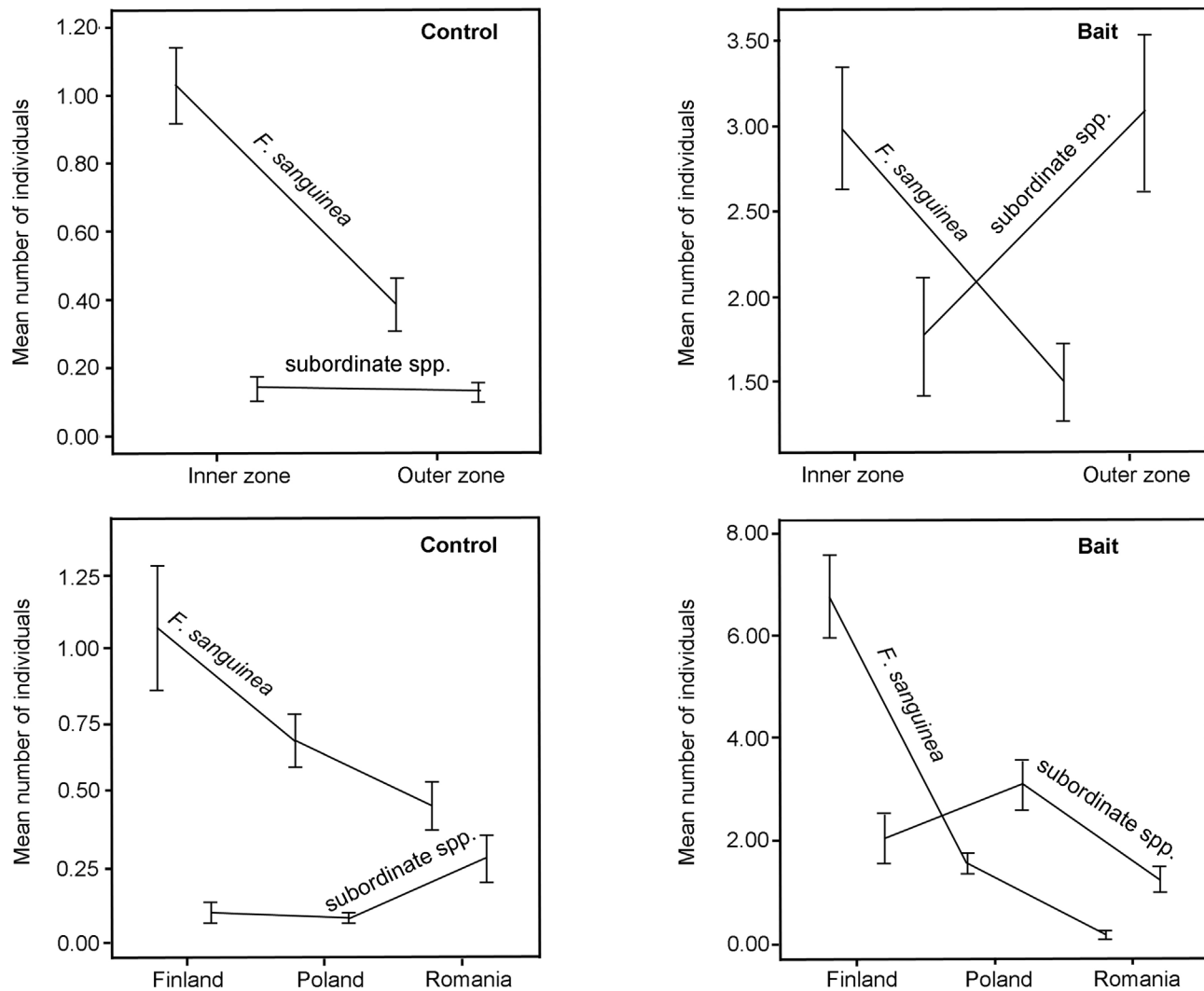


Fig. 3: The relationship between the abundance of *Formica sanguinea* workers and workers of subordinate species (mean values in the 95 % confidence interval) and the distance from the nest area border (inner and outer zone; at the top), and region (at the bottom) in the absence and in the presence of baits.

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 ex-

pected 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, GOTELLI & 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  $\chi^2$ -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 CORE TEAM 2016) with  $\alpha = 0.05$  significance level. All GLMMs were performed using the *glmer* and *glmer.nb* 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-

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

Output variable	Input variables and factors	Model outputs			
		Estimate	Standard error	z	p
Abundance of <i>F. sanguinea</i> – control	Observation zone	-1.13	0.20	-5.54	< 0.001
	Region (Finland vs. Poland)	-0.93	0.54	-1.71	0.26
	Region (Finland vs. Romania)	-1.65	0.58	-2.84	0.01
	Region (Poland vs. Romania)	-0.71	0.50	-1.43	0.42
Abundance of <i>F. sanguinea</i> – bait	Observation zone	-0.51	0.23	-2.16	0.03
	Region (Finland vs. Poland)	-3.95	0.52	-7.52	< 0.001
	Region (Finland vs. Romania)	-5.55	0.81	-6.84	< 0.001
	Region (Poland vs. Romania)	-1.59	0.79	-2.00	0.14
Abundance of subordinate species – control	Abundance of <i>F. sanguinea</i>	-0.03	0.05	-0.69	0.48
	Observation zone	-0.13	0.22	-0.57	0.56
	Region (Finland vs. Poland)	0.77	0.89	0.86	0.38
	Region (Finland vs. Romania)	0.51	0.88	0.57	0.56
Abundance of subordinate species – bait	Abundance of <i>F. sanguinea</i>	-0.27	0.01	-16.10	< 0.001
	Observation zone	0.72	0.28	2.56	0.01
	Region (Finland vs. Poland)	-0.30	1.58	-0.19	0.84
	Region (Finland vs. Romania)	-1.49	1.71	-0.87	0.38
Abundance of slaves – control	Abundance of <i>F. sanguinea</i>	0.09	0.02	3.44	0.00
	Observation zone	-0.00	0.31	-0.02	0.98
	Abundance of <i>F. sanguinea</i> × Observation zone	0.07	0.05	1.29	0.19
Abundance of slaves – bait	Abundance of <i>F. sanguinea</i>	0.06	0.01	3.56	0.00
	Observation zone	-0.27	0.41	-0.66	0.50
	Abundance of <i>F. sanguinea</i> × Observation zone	-0.06	0.02	-2.39	0.01

parisons with Tukey contrasts among the multiple factor levels when performing the GLMMs (HOTHORN & al. 2008). Czekanowski index was calculated with the help of *EcoSimR* package (GOTELLI & 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 *Formica 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 platythorax* as well as those of *F. rufibarbis* 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. 2: Bait discovery and exploitation (%) by *Formica sanguinea* and subordinate species around the investigated nests.

Country	Bait discovery / exploitation (%)	
	<i>F. sanguinea</i>	Subordinate species
Finland	100.00 / 84.37	78.00 / 37.00
Poland	67.00 / 26.13	69.00 / 42.00
Romania	60.00 / 2.50	62.00 / 12.50

significant differences were registered among the regions ( $\chi^2 = 1.06$ ,  $z \geq -0.87$ ,  $p \geq 0.38$ ; Fig. 3).

The temporal niche overlap index calculated for *Formica sanguinea* and subordinate ant species foraging around *F. 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. sanguinea* and subordinate ant species.

**The foraging activity of slaves in *F. sanguinea* colonies:** The abundance of *Formica sanguinea* workers was related to the abundance of *F. fusca* slaves (Fig. 4) both in the absence and in the presence of baits ( $z = 3.44$ ,  $p = 0.00$ ;  $z = 3.56$ ,  $p = 0.00$ , respectively; see Tab. 1). In the presence of these baits, the relationship between *F. 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. 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. 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 PISARSKI & VEPSÄLÄINEN 1989, CERDÁ & al. 2013). However, the results generally indicate the very plastic and variable competitive abilities of *F. sanguinea* during periods of their routine foraging activity (i.e., outside their raiding activity). In general, workers of *F. 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. 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 submissive and encounterers) within their territories. Even at baits, the negative influence of *F. 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.*

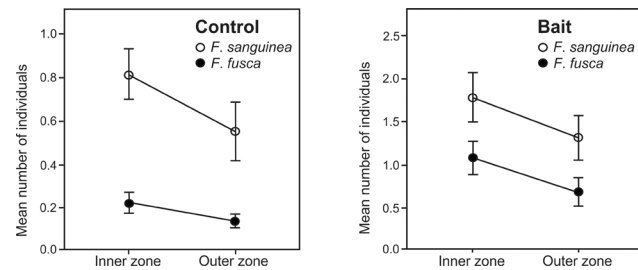


Fig. 4: The relationship between the abundance of *Formica sanguinea* workers and *F. fusca* slaves (mean values in the 95% confidence interval) and the distance.

*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. sanguinea* does not even exploit all the baits close to its nest. In typical territorial species (e.g., *Formica polyctena*, *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. sanguinea* (see e.g., SAVOLAINEN & VEPSÄLÄINEN 1988, VEPSÄLÄINEN & SAVOLAINEN 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. 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. 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. 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. 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 (PUNTTILA & 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., MARIKOVSKY 1974, COOL-KWAIT & TOPOFF 1984, MORI & al. 2001), which fulfil all daily tasks, including foraging. As a result, the slave species determines

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 *Raptiformica*, 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 intranidal 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 (DOBZĄŃSKI 1965, MORI & al. 2001). They can even directly participate in robbing pupae (DOBZĄŃSKI 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 DOBZĄŃSKI'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 (DOBZĄŃSKI 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., DOBZĄŃSKI 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 m<sup>2</sup> (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 SEIFERT'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 eradicate 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 STUBLE & 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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## References

- ADAMS, E.S. 2016: Territoriality in ants (Hymenoptera: Formicidae): a review. – *Myrmecological News* 23: 101-118.
- ADLER, F.R., LEBRUN, E.G. & FEENER, D.H. 2007: Maintaining diversity in an ant community: modeling, extending and testing the dominance-discovery trade-off. – *The American Naturalist* 169: 323-333.
- APPLE, J.L., LEWANDOWSKI, S.L. & LEVINE, J.L. 2014: Nest relocation in the slavemaking ants *Formica subintegra* and *Formica pergandei*: a response to host nest availability that increases raiding success. – *Insectes Sociaux* 61: 347-356.
- BATES, D., MAECHLER, M., BOLKER, B. & WALKER, S. 2014: `lme4`: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. – <http://CRAN.R-project.org/package=lme4>, retrieved on 20 July 2016.
- BUSCHINGER, A. 1990: Sympatric speciation and radiative evolution of socially parasitic ants – heretic hypotheses and their factual background. – *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 28: 241-260.
- BUSCHINGER, A. 2009: Social parasitism among ants. – *Myrmecological News* 12: 219-235.
- BUSCHINGER, A., EHRHARDT, W. & WINTER, U. 1980: The organization of slave raids in dulotic ants a comparative study (Hymenoptera: Formicidae). – *Zeitschrift für Tierpsychologie-Journal of Comparative Ethology* 53: 245-264.
- CERDÁ, X., ARNAN, X. & RETANA, J. 2013: Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology? – *Myrmecological News* 18: 131-147.
- CERDÁ, X., RETANA, J. & CROS, S. 1997: Thermal disruption of transitive hierarchies in Mediterranean ant communities. – *Journal of Animal Ecology* 66: 363-374.
- COOL-KWAIT, E. & TOPOFF, H. 1984: Raid organization and behavioral development in the slave-making ant *Polyergus lucidus* MAYR. – *Insectes Sociaux* 31: 361-374.
- CZECHOWSKI, W. 1977: Recruitment signals and raids in slave-maker ants. – *Annales Zoologici* 34: 1-26.
- CZECHOWSKI, W. 1996: Colonies of hybrids and mixed colonies; interspecific nest takeover in wood ants (Hymenoptera: Formicidae). – *Memorabilia Zoologica* 50: 1-116.
- CZECHOWSKI, W. 1998: Raids of *Formica sanguinea* LATR. as a factor conducive to colony founding by *Formica truncorum* FABR. (Hymenoptera: Formicidae). – *Annals of the Upper Silesian Museum* 8/9: 153-157.
- CZECHOWSKI, W. 1999: *Lasius fuliginosus* (LATR.) on a sandy dune – its living conditions and interference during raids of *Formica sanguinea* LATR. (Hymenoptera: Formicidae). – *Annales Zoologici* 49: 117-123.
- CZECHOWSKI, W. 2000: Interference of territorial ant species in the course of raids of *Formica sanguinea* LATR. (Hymenoptera: Formicidae). – *Annales Zoologici* 50: 35-38.
- CZECHOWSKI, W. 2004: Scarcity of sites suitable for nesting promotes plesiobiosis in ants (Hymenoptera: Formicidae). – *Entomologica Fennica* 15: 211-218.
- CZECHOWSKI, W., CZECHOWSKA, W. & VEPSÄLÄINEN, K. 2005: Structure and succession of *Lasius* s. str. (Hymenoptera: Formicidae) assemblages in a Finnish sand dune area – reassessment after taxonomic revisions of the subgenus. – *Entomologica Fennica* 16: 2-7.
- CZECHOWSKI, W. & MARKÓ, B. 2005: Competition between *Formica cinerea* MAYR (Hymenoptera: Formicidae) and co-occurring ant species, with special reference to *Formica rufa* L.: direct and indirect interferences. – *Polish Journal of Ecology* 53: 467-489.
- CZECHOWSKI, W. & MARKÓ, B. 2006: Uncomfortable protection: *Formica polyctena* FÖRST. shelters *Formica fusca* L. from *Formica sanguinea* LATR. (Hymenoptera: Formicidae). – *Annales Zoologici* 56: 539-548.
- CZECHOWSKI, W., MARKÓ, B. & GODZIŃSKA, E.J. 2009: Corpse carrying in ants (Hymenoptera: Formicidae): behavioural side effect of aggressive arousal or competitive signalling? – *Polish Journal of Ecology* 57: 341-352.
- CZECHOWSKI, W., MARKÓ, B., RADCHENKO, A. & ŚLIPIŃSKI, P. 2013: Long-term partitioning of space between two territorial species of ants (Hymenoptera: Formicidae) and their effect on subordinate species. – *European Journal of Entomology* 110: 327-337.
- CZECHOWSKI, W. & RADCHENKO, A. 2006: *Formica lusatica* SEIFERT, 1997 (Hymenoptera: Formicidae), an ant species new to Finland, with notes on its biology and the description of males. – *Myrmecological News* 8: 257-262.
- CZECHOWSKI, W., RADCHENKO, A., CZECHOWSKA, W. & VEPSÄLÄINEN, K. 2012: The ants (Hymenoptera: Formicidae) of Poland with reference to the myrmecofauna of Europe. – *Fauna Poloniae* vol. 4 (n.s.). Natura optima dux Foundation, Warszawa, 496 pp.
- CZECHOWSKI, W. & ROTKIEWICZ, W. 1996: Relations between *Formica sanguinea* LATR. and *Formica cinerea* MAYR (Hymenoptera: Formicidae) – an unusual form of dulosis. – *Annales Zoologici* 47: 469-478.
- DARWIN, C.R. 1859: On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. – John Murray, London, 502 pp.
- DE BISEAU, J.C. & PASTEELS, J.M. 2000: Response thresholds to recruitment signals and the regulation of foraging intensity in the ant *Myrmica sabuleti* (Hymenoptera: Formicidae). – *Behavioural Processes* 48: 137-148.
- DE BISEAU, J.C., QUINET, Y., DEFFERNEZ, L. & PASTEELS, J.M. 1997: Explosive food recruitment as a competitive strategy in the ant *Myrmica sabuleti* (Hymenoptera: Formicidae). – *Insectes Sociaux* 44: 59-73.
- DE BRUYN, G.J. & MABELIS, A.A. 1972: Predation and aggression as possible regulatory mechanisms in *Formica*. – *Ekologia Polska* 20: 93-101.
- D'ETTORRE, P. & HEINZE, J. 2001: Sociobiology of slave-making ants. – *Acta Ethologica* 3: 67-82.
- DOBZAŃSKI, J. 1961: Sur l'éthologie guerrière de *Formica sanguinea* LATR. (Hymenoptère: Formicidae). – *Acta Biologicae Experimentalis* 21: 53-73.
- DOBZAŃSKI, J. 1965: Genesis of social parasitism among ants. – *Acta Biologicae Experimentalis* 25: 59-71.
- DOMISCH, T., FINÉR, L. & JURGENSEN, M.F. 2005: Red wood ant mound densities in managed boreal forests. – *Annales Zoologici Fennici* 42: 277-282.
- DRIESSEN, G.J.J., VAN RAALTE, A.T. & DE BRUYN, G.J. 1984: Cannibalism in the red wood ant, *Formica polyctena* (Hymenoptera: Formicidae). – *Oecologia* 63: 13-22.

- GALLÉ, L. 1991: Structure and succession of ant assemblages in a north European sand dune area. – *Holarctic Ecology* 14: 31-37.
- GOTELLI, N.J., HART, E.M. & ELLISON, A.M. 2015: EcoSimR: null model analysis for ecological data. R package version 0.1.0. – <<http://github.com/gotellilab/EcoSimR>>, retrieved on 1 August 2018.
- GIBB, H. & JOHANSSON, T. 2011: Field tests of interspecific competition in ant assemblages: revisiting the dominant red wood ants. – *Journal of Animal Ecology* 80: 548-557.
- GIBB, H. & PARR, C.L. 2010: How does habitat complexity affect foraging success? A test using functional measures on three continents. – *Oecologia* 164: 1061-1073.
- HOTHORN, T., BRETZ, F. & WESTFALL, P. 2008: Simultaneous inference in general parametric models. – *Biometrical Journal* 50: 346-363.
- HÖLDOBLER, B. & WILSON, E.O. 1990: The ants. – Harvard University Press, Cambridge, MA, 732 pp.
- KHARKIV, V.A. 1997a: Effectiveness of activity and division of labour between slaves and slavemakers in colonies of *Formica sanguinea* (Hymenoptera: Formicidae). – *Zoologicheskij Zhurnal* 76: 438-443.
- KHARKIV, V.A. 1997b: Competition as a mechanism of division of labour in colonies of ant slavemakers *Formica sanguinea* (Hymenoptera: Formicidae). – *Zoologicheskij Zhurnal* 76: 444-447.
- KING, J.R. & TRAGER, J.C. 2007: Natural history of the slave making ant, *Polyergus lucidus*, sensu lato in northern Florida and its three *Formica pallidefulva* group hosts. – *Journal of Insect Science* 7: art. 42.
- MAÁK, I., MARKÓ, B., ERŐS, K., BABIK, H., ŚLIPŃSKI, P. & CZECHOWSKI, W. 2014: Cues or meaningless objects? Differential responses of the ant *Formica cinerea* to corpses of competitors and enslavers. – *Animal Behaviour* 91: 53-59.
- MABELIS, A.A. 1979: Wood ant wars. The relationship between aggression and predation in the red wood ant (*Formica polyctena* Foerst.). – *Netherlands Journal of Zoology* 29: 451-620.
- MARIKOVSKY, P.I. 1974: The biology of the ant *Rossomyrmex* W. ARNOLDI (1928). – *Insectes Sociaux* 21: 301-308.
- MARKÓ, B. & CZECHOWSKI, W. 2004: *Lasius psammophilus* SEIFERT and *Formica cinerea* MAYR (Hymenoptera: Formicidae) on sand dunes: conflicts and coexistence. – *Annales Zoologici* 54: 365-378.
- MARKÓ, B. & CZECHOWSKI, W. 2012: Space use, foraging success and competitive relationships in *Formica cinerea* (Hymenoptera: Formicidae) on sand dunes in southern Finland. – *Ethology, Ecology and Evolution* 24: 149-164.
- MARKÓ, B., CZECHOWSKI, W. & RADCHENKO, A. 2013: Combining competition with predation: drastic effect of *Lasius fuliginosus* (LATR.) on subordinate ant species at the northern limit of its distribution. – *Annales Zoologici* 63: 107-111.
- MARKÓ, B., CZEKES, ZS., ERŐS, K., CSATA, E. & SZÁSZ-LEN, A.-M. 2012: The largest polydomous system of *Formica* ants (Hymenoptera: Formicidae) in Europe discovered thus far in Romania. – *North-Western Journal of Zoology* 8: 287-291.
- MORI, A., GRASSO, D.A. & LE MOLI, F. 2000: Raiding and foraging behavior of the blood-red ant, *Formica sanguinea* LATR. (Hymenoptera: Formicidae). – *Journal of Insect Behavior* 13: 421-438.
- MORI, A., GRASSO, D.A., VISICCHIO, R. & LE MOLI, F. 2001: Comparison of reproductive strategies and raiding behaviour in facultative and obligatory slave-making ants: the case of *Formica sanguinea* and *Polyergus rufescens*. – *Insectes Sociaux* 48: 302-314.
- PALMGREN, P. 1972: Studies on the spider populations of the surroundings of the Tvärminne Zoological Station, Finland. – *Societas Scientiarum Fennica – Commentationes Biologicae* 52: 1-133.
- PETRÁKOVÁ, L. & SCHLAGHAMERSKÝ, J. 2011: Interactions between *Liometopum microcephalum* (Formicidae) and other dominant ant species of sympatric occurrence. – *Community Ecology* 12: 9-17.
- PISARSKI, B. & VEPSÄLÄINEN, K. 1989: Competition hierarchies in ant communities (Hymenoptera, Formicidae). – *Annales Zoologici* 42: 321-329.
- PUNTTILA, P., HAILA, Y. & TUKIA, H. 1996: Ant communities in taiga clearcuts: habitat effects and species interactions. – *Ecography* 19: 16-28.
- PUNTTILA, P., NIEMELÄ, P. & KARHU, K. 2004: The impact of wood ants (Hymenoptera: Formicidae) on the structure of invertebrate community on mountain birch (*Betula pubescens* ssp. *czerepanovii*). – *Annales Zoologici Fennici* 41: 429-446.
- R CORE TEAM 2016: R: a language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria; <<https://www.R-project.org/>>, retrieved on 4 November 2016.
- RETANA, J., ARNAN, X. & CERDÁ, X. 2015: A multidimensional functional trait analysis of resource exploitation in European ants. – *Ecology* 96: 2781-2793.
- REZNIKOVA, Z.I. 1980: Mezhhvidovaya ierarkhiya u murav'ev. – *Zoologicheskij Zhurnal* 59: 1168-1176.
- REZNIKOVA, Z.I. 1983: Mezhhvidovye otnosheniya murav'ev.– Nauka, Novosibirsk, 206 pp.
- SANDERS, N.J. & GORDON, D.M. 2003: Resource-dependent interactions and the organization of desert ant communities. – *Ecology* 84: 1024-1031.
- SAVOLAINEN, R. & DESLIPPE, R.J. 1996: Facultative and obligate slavery in formicine ants: frequency of slavery, and proportion and size of slaves. – *Biological Journal of the Linnean Society* 57: 47-58.
- SAVOLAINEN, R. & VEPSÄLÄINEN, K. 1988: A competition hierarchy among boreal ants: impact on resource partitioning and community structure. – *Oikos* 51: 135-155.
- SAVOLAINEN, R. & VEPSÄLÄINEN, K. 1989: Niche differentiation of ant species within territories of wood ant *Formica polyctena*. – *Oikos* 56: 3-16.
- SAVOLAINEN, R., VEPSÄLÄINEN, K. & WUORENRIINNE, H. 1989: Ant assemblages in the taiga biome: testing the role of territorial wood ants. – *Oecologia* 81: 481-486.
- SEIFERT, B. 1987: A model to estimate interspecific competitive displacement in ants (Hymenoptera, Formicidae). – *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere* 114: 451-469.
- STUBLE, K.L., JURIC, I., CERDÁ, X. & SANDERS, N.J. 2017: Dominance hierarchies are a dominant paradigm in ant ecology (Hymenoptera: Formicidae), but should they be? And what is a dominance hierarchy anyways? – *Myrmecological News* 24: 71-81.
- ŚLIPŃSKI, P., CZECHOWSKI, W., MARKÓ, B., RZESZOWSKI, K. & BABIK, H. 2014: *Lasius fuliginosus* (Hymenoptera: Formicidae) shapes local ant assemblages. – *North-Western Journal of Zoology* 10: 404-412.
- ŚLIPŃSKI, P. & ŽMIHORSKI, M. 2017: Changes in the speed of ants as a result of aggressive interactions. – *Insect Science* 24: 842-852.
- TRIGOS PERAL, G., MARKÓ, B., BABIK, H., TÁUSAN, I., MAÁK, I., PÁLFI, Z., ŚLIPŃSKI, P., CZEKES, Z. & CZECHOWSKI, W. 2016: Differential impact of two dominant *Formica* ant species (Hymenoptera: Formicidae) on subordinates in temperate Europe. – *Journal of Hymenoptera Research* 50: 97-116.
- VÄÄNÄNEN, S., VEPSÄLÄINEN, K. & SAVOLAINEN, R. 2010: Indirect effects in boreal ant assemblages: territorial wood ants protect potential slaves against enslaving ants. – *Annales Zoologici* 60: 57-67.

- VEPSÄLÄINEN, K. & CZECHOWSKI, W. 2014: Against the odds of the ant competition hierarchy: submissive *Myrmica rugulosa* block access of the dominant *Lasius fuliginosus* to its aphids. – *Insectes Sociaux* 61: 89-93.
- VEPSÄLÄINEN, K. & PISARSKI, B. 1982: Assembly of island ant communities. – *Annales Zoologici Fennici* 19: 327-335.
- VEPSÄLÄINEN, K. & SAVOLAINEN, R. 1990: The effect of interference by formicine ants on the foraging of *Myrmica*. – *Journal of Animal Ecology* 59: 643-654.
- WITTMAN, S.E. & GOTELLI, N.J. 2011: Predicting community structure of ground-foraging ant assemblages with Markov models of behavioral dominance. – *Oecologia* 166: 207-219.
- WITTMAN, S.E., SANDERS, N.J., ELLISON, A.M., JULES, E.S., RATCHFORD, J.S. & GOTELLI, N.J. 2010: Species interactions and thermal constraints on ant community structure. – *Oikos* 119: 551-559.
- ŽMIHORSKI, M. & ŚLIPIŃSKI, P. 2016: The importance of diurnal and nocturnal activity and interspecific interactions for space use by ants in clear-cuts. – *Ecological Entomology* 41: 276-283.