Parasitic relationship between the fungus *Rickia wasmannii (*Ascomycota: Laboulbeniales) and the ant *Myrmica scabrinodis*: behavioral modifications and defense mechanisms.

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1. Ants and their parasites

Pathogens, parasites and their hosts provide excellent models for studies on coevolution. They are intrinsically linked but their evolutionary interests are different. Selection on the pathogen is for greater exploitation of the host and selection on the host is for exclusion of the pathogen (Bush *et al*., 2001). Behavioural changes are known from a wide range of host/parasites interactions (Hindsbo, 1972; Curtis, 1987; Combes, 1991; Lafferty and Morris, 1996; Poulin, 1998; Poulin and Thomas, 1999; Berdoy *et al*., 2000; Moore, 2002).

However, not just unitary organisms can have parasites or behavioral manipulation by parasites, but also the behavior of the superorganisms, as e.g. societies of eusocial insects, can be affected, altered by parasites (Hölldobler and Wilson, 1990, 2009). Ants are frequently targeted by parasites, and in some cases parasitic organisms induce changes in the life history, physiology and behavior of the ant hosts (Schmid-Hempel, 1998). The social life of ants implies high frequency of contacts among nestmates, that increases the risk of spreading of any pathogen and parasite among colony members. In addition, the existence of overlapping generations enables the transmission and persistence of parasites and pathogens vertically, through generations as well (Hamilton, 1987; Schmid-Hempel, 1998; Baer and Schmid-Hempel, 1999). There are a lots of different organisms that parasitize ants, like the intracellular endosymbiont *Wolbachia* spp. (Keller *et al*., 2001; Dedeine *et al*., 2005), the flukeworm *Dicrocoelium* spp. (Spindler *et al*., 1986; Manga-Gonzalez *et al*., 2001), nematodes (Poinar and Yanoviak, 2008; Csősz and Majoros, 2009), mites (Bruce and LeCato, 1980), larvae of *Maculinea* butterflies (Witek *et al*., 2010), the dipteran *Microdon* spp. (Witek *et al*., 2014), and fungi in addition (Pontoppidan *et al*., 2009; Espadaler and Santamaria, 2012; Haelewaters *et al*., 2012; Csata *et al*., 2013; Csata *et al*., 2014).

To defend themselves, ants have evolved a variety of adaptations against parasites, including behavioral, biochemical and immunological responses to reduce virulence and transmission of entomopathogen agents. More specifically, against the fungi within the colony, such as the production of antibiotics by the metapleural and other glands, increased auto- and allogrooming, nest cleaning, pathogen avoidance, isolation of parasite's propagules (social encapsulation), removal of infected individuals, waste management, and sometimes even the relocation of the entire colony (Howard and Tschinkel, 1976; Schmid-Hempel, 1998; Hart and Ratnieks, 2002; Soeprono and Rust, 2004, Boomsma *et al*., 2005; Roy *et al*., 2006;

Schlüns and Crozier, 2009; Wilson-Rich *et al.*, 2009; Konrad *et al.*, 2012; Ortiz- Urquiza and Keyhani, 2013; Otti *et al.*, 2014).

Among ant parasitic organisms, fungi are one of the most diverse groups, with respect to both systematics and lifestyle (Weir and Blackwell, 2005; Roy *et al.*, 2006). Fungi display a wide variety of interactions with ants from transient to obligate associations Some are known to be lethal to the host, whereas others are considered to be close to neutral, but in several cases the insect, the fungus, or both may benefit from their interaction (Vega *et al.*, 2009; Blackwell, 2010). Fundamental research has focused on many theoretical and practical aspects of their biology, physiology, ecology, and epidemiology, but predominantly from the viewpoint of their potential in host population regulation. Recently, Espadaler and Santamaria (2012) offered a comprehensive survey of myrmecoparasitic fungi present in Europe. In Romania there were only sporadic if ever studies about the myrmecopathogenic fungi (Paşcovici, 1983). In the frame of my thesis I will summarize the current knowledge on the myrmecopathogenic fungi of Romania, and I will specifically focus on the distribution, prevalence and effects of *Rickia wasmannii*, a myrmecoparasitic fungus from the order Laboulbeniales.

2. Aims of the study

During our study we investigated the host-parasite relationship between the ectoparasitic fungus *Rickia wasmannii* and its host ant *Myrmica scabrinodis*. The aims of this thesis were to elaborate on the ways a fungal infection can affect the ant host's behavior.

3. Study species

In Europe there are just few ant parasitize fungus species, most of which are insufficiently known. Only scarce data is available on their phylogenetic position, geographic range, host specificity and on their effect on the host (Bezděčka and Bezděčková, 2011; Lapeva-Gjonova and Santamaría, 2011; Espadaler and Santamaría, 2012; Csata *et al.*, 2013; Báthori *et al.*, 2014; Haelewaters *et al.*, 2015).

In Romania currently we know five myrmecopathogenic fungal species: *Aegeritella superficialis*, *Myrmicinosporidium durum*, *Pandora myrmecophaga*, *Laboulbenia camponoti* and *Rickia wasmannii* (Espadaler and Santamaría, 2012; Csata *et al.*, 2013; Báthori *et al.*, 2014).

Pandora myrmecophaga (Turian et Wuest) S. Keller (2005)

Pandora myrmecophaga is also member of the subphylum Entomophthoromycotina. The fungus produces infective spores that attach to, germinate on, and penetrate the cuticle of its hosts, ultimately killing them. The fungal mycelium grows in the head, mesosoma, gaster, antennae, and legs of the ant. The fungus is quite widely distributed in Europe. In Romania it is reported for the first time. It was found on *Formica exsecta* near the După Luncă protected marshland area at Voşlobeni in Harghita County (Fig. 1).

Aegeritella superficialis Bałazy et J. Wiśn. (1974)

Aegeritella superficialis is one of the five known *Aegeritella* species (Pezizomycotina, Ascomycota). All of them grow on the cuticle of workers of *Formica* species (Espadaler and Wiśniewski, 1987; Espadaler and Monteserín, 2003; Espadaler and Santamaria, 2012). They are believed to be epizoic fungi, since the contact of the fungus with the insect cuticle is superficial. Based on available data it can be considered to be the most widely distributed myrmecoparasitic fungi in Romania. In a single article Paşcovici (1983) reported it on *Formica polyctena* Foerster, 1850, *F. pratensis* Retzius, 1783 and *F. rufa* Linnaeus, 1761 from nine localities (Fig. 1).

Myrmicinosporidium durum Hölldobler, 1933

The true systematic position of this fungus is still not clear (Sanchez-Peña *et al.*, 1993; Espadaler and Santamaría, 2012), but it is a member of the subphylum Entomophthoromycotina (the former order Entomophthorales). Infected ants are easy to recognize based on their conspicuous appearance: their body contain numerous dark, lentiform capsules (ca. 30-50 µm in diameter), and these thickwalled spores of the fungi can easily be seen through the cuticle under a microscope (Sanchez-Peña *et al.*, 1993; Buschinger *et al.*, 2004; Pereira, 2004, Gonçalves *et al.*, 2012). The fungus is quite widely distributed in Europe. In Romania it was recently discovered in two different species at three separate locations (Csősz *et al.*, 2012) (Fig. 1).

Laboulbenia camponoti S. W. T. Batra 1963

Fungus *L. camponoti* is a member of the phylum Ascomycota, order Laboulneniales. They are obligate external parasites of arthropods, especially insects (Tavares, 1985; Santamaría, 1998). The distribution of the fungus is from Asia to Europe. In Romania Báthori *et al*., (2014) reported it from Baziaș (Fig. 1).

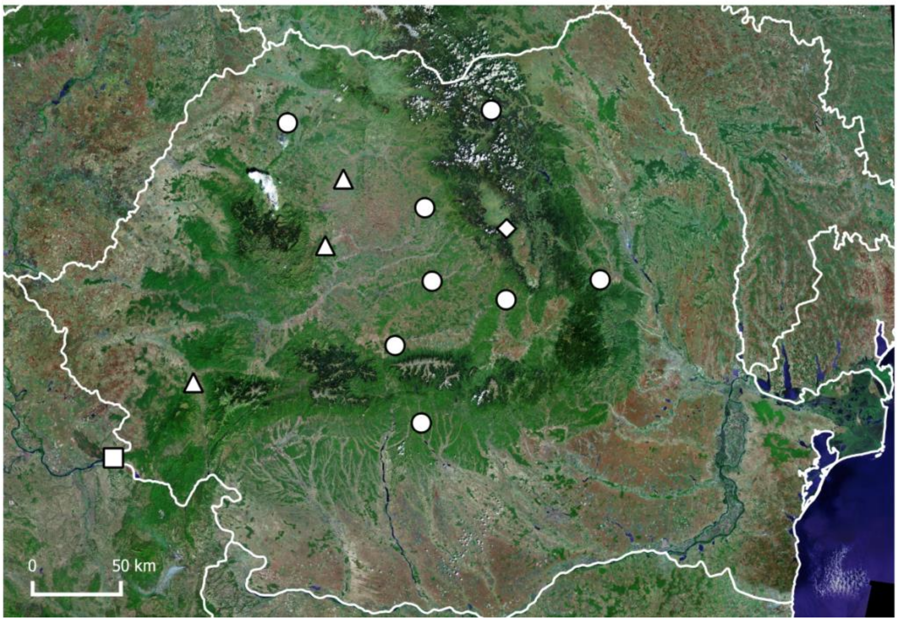

Fig. 1. Currently known distribution of *Aegeritella superficialis* (white dot), *Myrmicinosporidium durum* (white triangle), *Pandora myrmecophaga* (white diamond) and *Laboulbenia camponoti* (white square).

The other Laboulbenian fungus, which is known from Romania is *Rickia wasmannii*, a widely distributed fungus in Europe. This fungus and it's interaction with the host species *Myrmica scabrinodis* are presented in my thesis.

3.1. The minute mistery: *Rickia wasmannii* Cavara, 1899

The fungus *Rickia wasmannii* was understudied for a long time but in recent years more reports about its distribution and host ant usage have been published, and these have shown *R. wasmannii* to be the most widely distributed of the four ant-parasitizing Laboulbeniales species in Europe (Fig. 2., Espadaler and Santamaria, 2012; Haelewaters, 2012, Csata *et al*., 2013, 2014; Haelewaters *et. al*., 2015; Santamaría and Espadaler, 2015; Báthori *et al*., 2014, 2015).

Fig. 2. *M. scabrinodis* worker infected with *R. wasmannii* (SEM photo taken with JSM-5510 by Ciprian Mihali).

The fungal thalli penetrate the outer layer of the cuticle, and appear on the surface of the hosts as clubbed setae-like structures under the stereoscope (Fig. 2). This makes the infected host easy to recognize for the myrmecologist, as highly infected ants appear unusually hairy (Fig. 2).

Little is known about the effect of the Laboulbeniales fungi on their hosts, and while the fungi are parasitic and penetrate to the hemocoel of the host, they have been usually regarded as neutral (see Tartally *et al*., 2007; García *et al*., 2010; Lapeva-Gjonova and Santamaría, 2011; Bezděčka and Bezděčková, 2011; Espadaler and Santamaría, 2012).

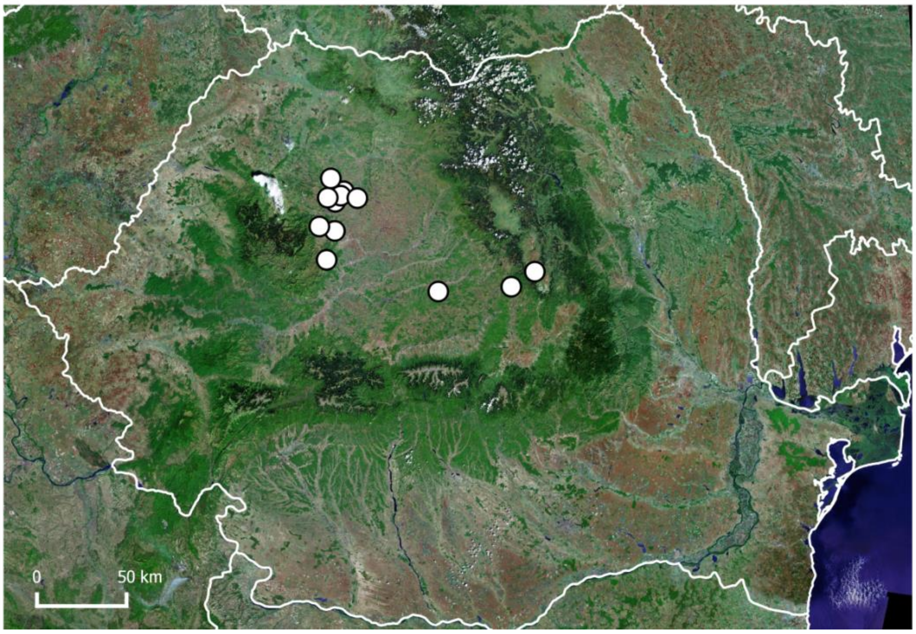

Fig. 6. Currently known distribution of the ectoparasitic fungus *Rickia wasmannii* in Romania (the known 12 populations).

3.2. The most common ant host in Romania: *Myrmica scabrinodis*

One of the most widely distributed Euro- Siberian member is *M. scabrinodis* inhabiting moderately humid open habitat. It uses a wide variety of habitats, it is most commonly associated with grasslands but it also can occurs in open forests and woodlands. It tolerates high soil moisture but needs high solar insolation and thus often occurs in peat bogs in the temperate region. Colonies usually build large solarium from soil, where they rear their larvae. Nests are mostly built in the ground, in grass or moss tufts. Colonies are monogynous or with a few queens, containing up to 2500 workers (Radchenko and Elmes, 2010).

4. Study sites

Collections of study species were carried out at three locations in Cluj County, Romania (Luna de Jos, Fînațele Clujului and Borșa Cătun). The sites are meadows of northern exposure consisting of a mosaic of dry and moist patches. The sites Luna de Jos and Borșa Cătun are mostly covered by meso-xeric grasslands (dominated by *Festuca rupicola*, *Brachypodium pinnatum*, *Agrostis tenuis*, *Poa angustifolia*) rich in dicotyledonous species (e.g. *Dorycnium* *herbaceum*, *Filipendula vulgaris*, *Salvia pratensis*). The other site at Fânațele Clujului is a semi-dry basiphilous grassland dominated by *Festuca rupicola*, *Brachypodium pinnatum*, *Elymus hispidus*, *Agrostis capillaris*, *Carex michelii*, and a high representation of *Filipendula vulgaris*, *Adonis vernalis*, *Salvia pratensis*, *Clematis recta*, *Plantago media*, *Lotus corniculatus* and *Trifolium montanum*.

5. Results

5.1. Distribution of the myrmecoparasitic fungus *Rickia wasmannii* (Ascomycota: Laboulbeniales) across colonies, individuals, and body parts of *Myrmica scabrinodis*

In this chapter our aim is to provide information on the prevalence and distribution of this fungus across different spatial scales – colonies, individuals, and body parts of individuals. Moreover, we compare infection levels between different habitat types (wet versus dry) and also between different parts of the infected colonies (above- versus below-ground) to explore whether infected ants occur under specific environmental conditions or in specific age or task classes of ants, which reside in different parts of the nest (e.g. older individuals and foragers are usually located in the outer perimeter).

The general assumption of our study is that in order to obtain a fairly accurate view of a parasite's distribution within eusocial hosts one needs to extend investigations to several different levels of organizational hierarchy. Through our present study, infections were restricted to a single host species, *Myrmica scabrinodis*, and infected colonies were mostly concentrated in moist habitats. Individual infections exhibited the aggregated (biased) distributions typical to host-parasite systems. The GLMM analysis indicated that habitat type (wet versus dry) did not influence significantly the parasitic load of infected individuals (Fig. 3. GLMM $t = 0.8$, $p = 0.42$). On the other hand, within-colony prevalence showed clear spatial bias within nests. Within infected colonies, workers collected from the below-ground part of nests carried less fungi than those collected from the above-ground solaria (GLMM $t = -3.25$, $p < 0.001$; Fig. 4)

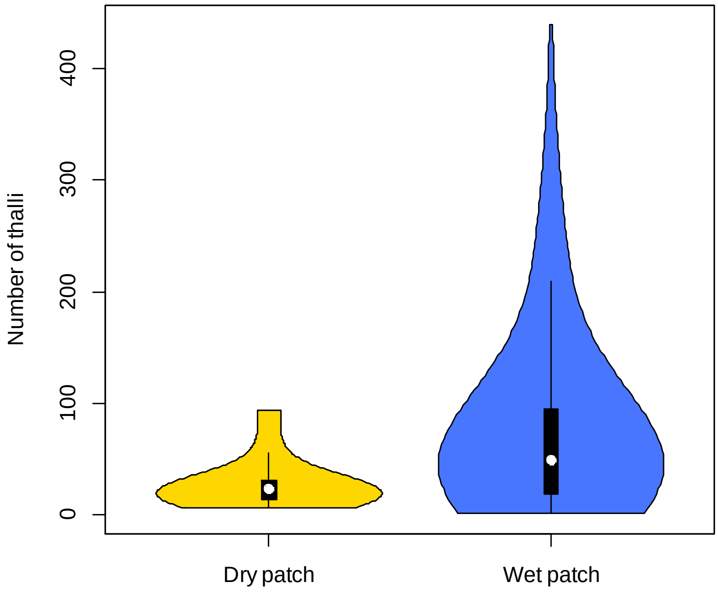

Fig. 3. Differences in the intensity of infection between ant workers from dry-, and wet-patches (median, quartiles, min-max values).

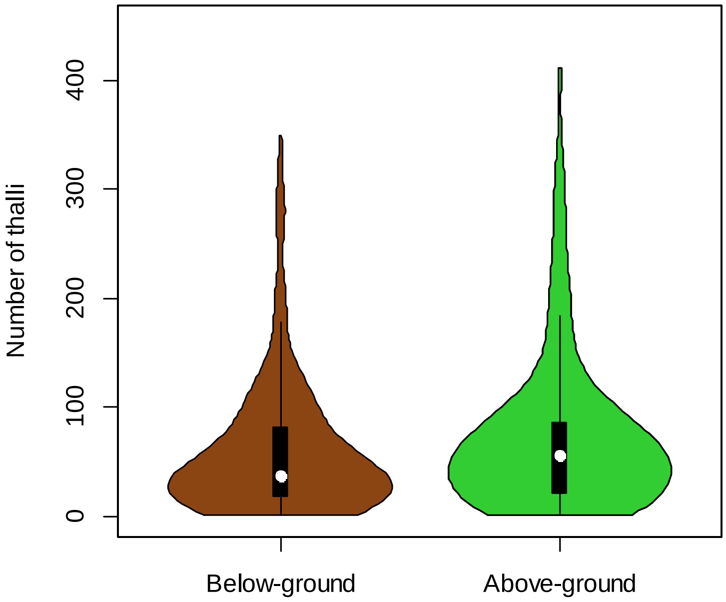

Fig. 4. Differences in the intensity of infection between ant workers from below-, and above-ground parts of the ant nests (median, quartiles, min-max values).

The distribution of fungi among host body parts statistically differed between low-intensity versus high-intensity infections. *Rickia wasmannii* was present on the surfaces of all major body parts from the mandibles and antennae to the abdomen, in some extreme cases even the eyes were invaded. Its frequency distribution showed a bias to the head and abdomen in particular (Fig. 5).

Since the present study is the first to outline a descriptive ecology for the occurrence of *Rickia wasmannii* in natural habitats and across wide range of hierarchical levels (habitats, colonies, individuals, body parts), we can make no comparisons to other studies on this myrmecoparasitic fungi only to research carried out on other Laboulbeniales. Rather we hope that the present results may provide baseline data for future comparative or monitoring studies.

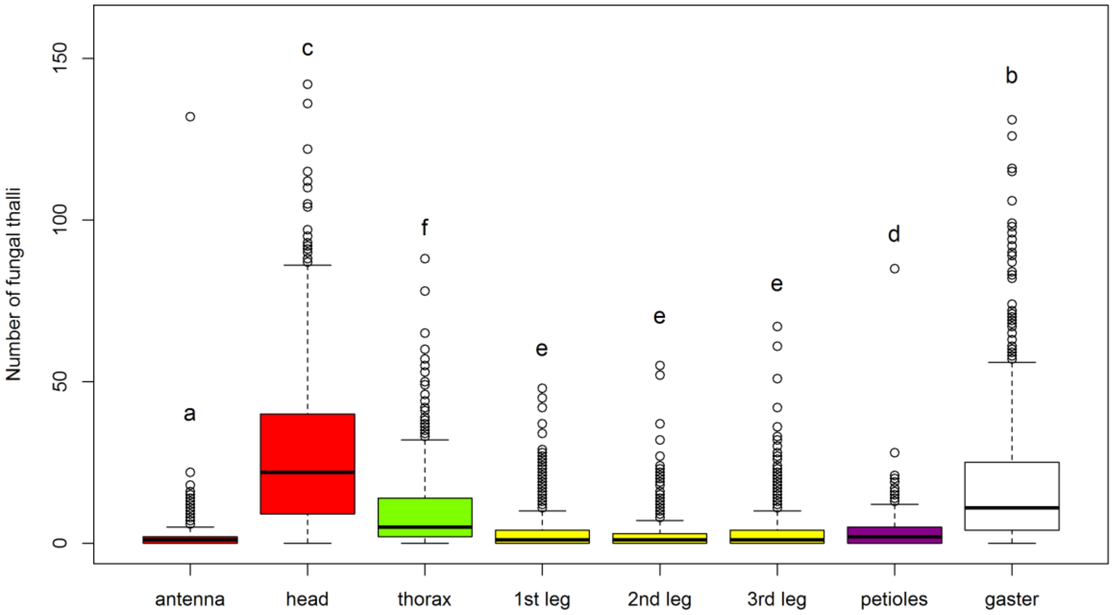

Fig. 14. Infection intensity on different body parts of ant workers (median, quartiles, min-max values) (GLMM, $\chi^2 = 7538.3$, $p < 0.0001$). Different letters indicate significant differences among groups ($t \geq 3.72$, $p < 0.001$).

Being unable to measure the surface areas of different body parts, we could not test whether the detected pattern differed from the one expected by chance. The proportion (thalli on the head / thalli on the abdomen) was significantly negatively influenced by the intensity of the infection ($F = 4.36$, $R^2 = 0.0089$, $p = 0.03$).

5.2. Effects of the ectoparasitic fungus *Rickia wasmannii* on its ant host *Myrmica scabrinodis*: changes in host mortality and grooming behavior

The exceptionally high abundance of *R. wasmannii* thalli on the host cuticle (see Markó *et al*., subm.) and the absence of pathogenicity data led us to investigate in laboratory conditions whether the parasite may induce changes in the behavior of the host while also affecting its lifespan. Our results show that the infected ants had significantly reduced lifespan according to the results of the Cox regression analyses (Fig. 5.): Cox coefficient = 0.62, z = -2.86, p < 0.004.

The frequency of autogrooming within a nest was significantly enhanced by the presence of infection (z = 4.02, p < 0.001), Infected workers spent also more time by autogrooming than uninfected individuals (z = 4.17, p < 0.001).

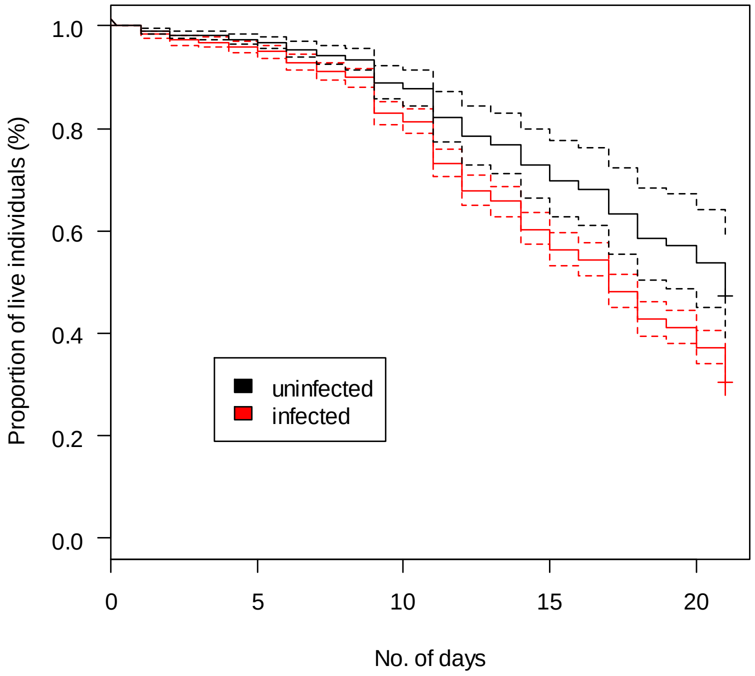

Fig. 18. Estimated functions for Cox regression of survival time based on the infection status of *M. scabrinodis* workers. Broken lines represent a point-wise 95 % confidence interval around the corresponding functions

In the case of the allogrooming, the GLMM analyses yielded similar results. Thus, the infection increased significantly the frequency of allogrooming within a nest (Fig. 5. z = 3.65, p < 0.001), also the time (z = 3.1, p < 0.001).

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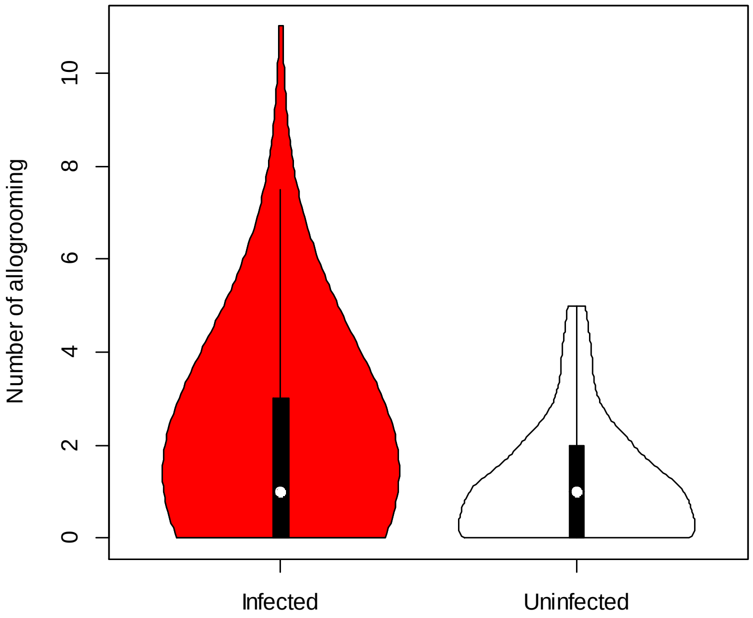


The frequency of allogrooming in infected and uninfected *M. scabrinodis*

We did not find significant differences between the time elapsed until discovery on infected (II) and uninfected (IU) corpses in the case of infected *M. scabrinodis* colonies (Fig. 6. Cox coeff = 1.05, z = 0.10, p = **NS**, n = 27), and also infected (UI) and uninfected (UU) corpses where the *M. scabrinodis* colonies were uninfected (Cox coeff = 1.42, z = 0.77, p = **NS**, n = 27, Fig.6).

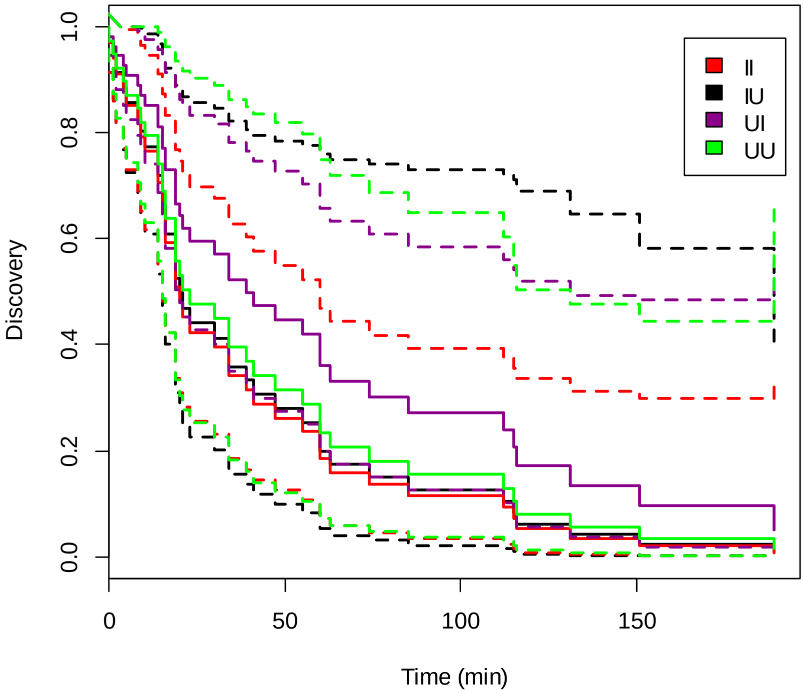


Fig. 6. Time elapsed until the discovery of infected and uninfected corpses (UI = infected colonies with uninfected corpses, II = infected colonies with infected corpses, UI = uninfected colonies with infected corpses, and UI = uninfected colonies with uninfected corpses).

5.3. Lockpick to the society: fungal infection facilitates the intrusion of strangers into ant colonies

The main aim of our work was to assess the effect of *Rickia wasmannii* infection on *Myrmica scabrinodis* host ant's behavior and on its interactions with other organisms. Specifically, we investigated: (1) nest-mate discrimination ability of infected and uninfected ant workers based on aggressiveness towards non-nestmates coming from infected and uninfected colonies; (2) behavior of infected and uninfected workers towards unrelated queens, (3) behavior of infected and uninfected workers toward other co-occurring, thus potentially rival ant species, like *Lasius flavus* and *Tetramorium* cf. *caespitum.* No aggressive interactions were recorded in the control experiments when intracolonial aggression was tested. Thus, irrespective of their infection status *Myrmica scabrinodis* workers behaved neutrally or positively towards their nest-mates in all cases.

Aggression between non-nestmates was significantly lower in the case when both ant workers were infected (I-I) in comparison to encounters where only one of the workers was infected (I-UI) or when both were uninfected (UI-UI) ($z \geq 2.47$, $p \leq 0.03$; Fig. 7)._There was no significant difference between the two latter groups (I-UI vs UI-UI $z = 0.64$, p = NS).

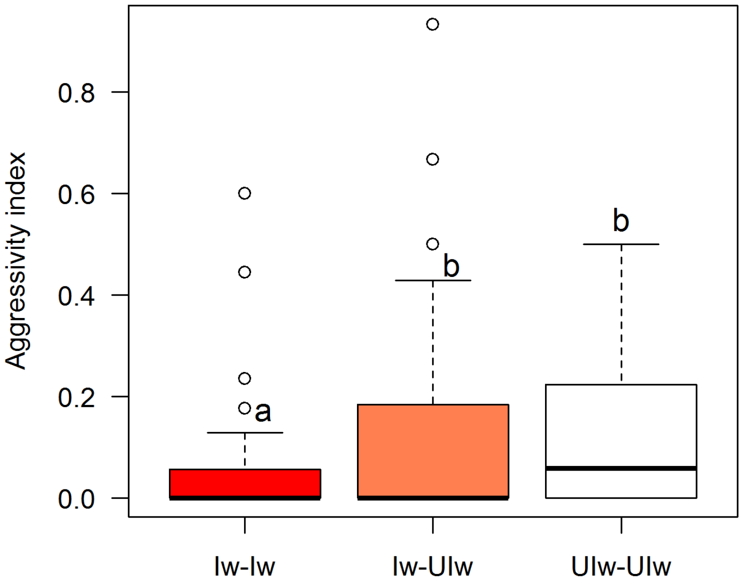
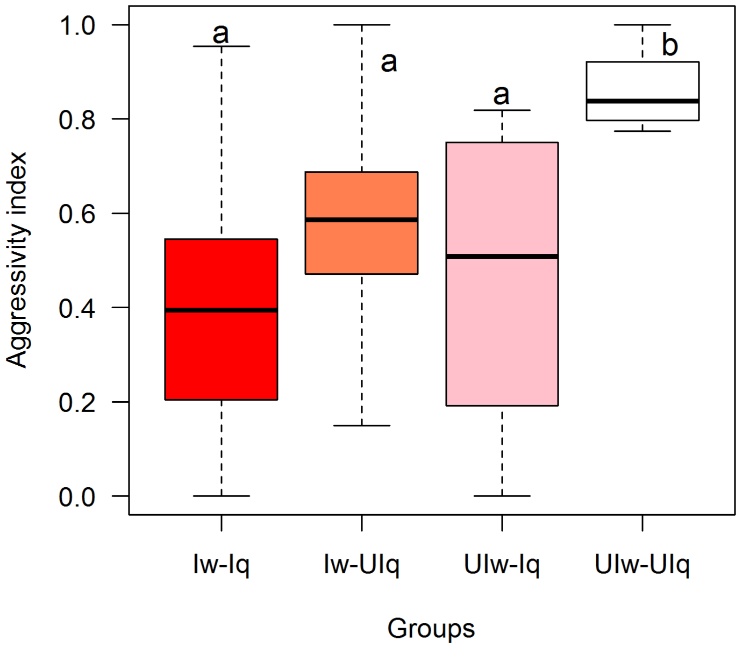


Fig. 7. Aggression index between *M. scabrinodis* workers of different infection status: I – infected by *R. wasmannii*, UI – uninfected (median, quartiles, and min-max values).

The aggression of workers towards foreign queens was significantly higher in the case when both workers and queen were coming from unifected colonies ($z \geq 3.274$, $p < 0.001$; Fig. 8), whereas no differences were found among groups where at least one partner (queen or workers) or both partners were infected by the fungus ($z \leq 1.34$, p = NS; Fig. 8). When the aggression of queens towards workers was analyzed the UI-UI combinations also displayed significantly higher aggression than the I-I combinations ($z = 2.72$, $p = 0.03$), but there were no differences with regards to groups at which at least one partner was infected (I-UI and UI-I groups) ($z \leq 1.10$, p = NS)



Aggression index between *M. scabrinodis* queens (q) and workers (w) of different infection status: I – infected by *R. wasmannii*, UI – uninfected (median, quartiles, min-max values).

The infection status of the *M. scabrinodis* workers did not influence significantly the agressivity towards *Lasius flavus* individuals (z = -0.68, p = NS) and toward *T.* cf. *caespitum* (z = -1.19, p = NS). Also we did not find significance difference between the agressivity of the *L. flavus* workers toward infected or uninfected *M. scabrinodis* workers (z = -0.76, p = NS), or no significant differences in the agressivity of the *Tetramorium* workers toward infected or uninfected *M. scabrinodis* workers (z = -1.0, p = NS).

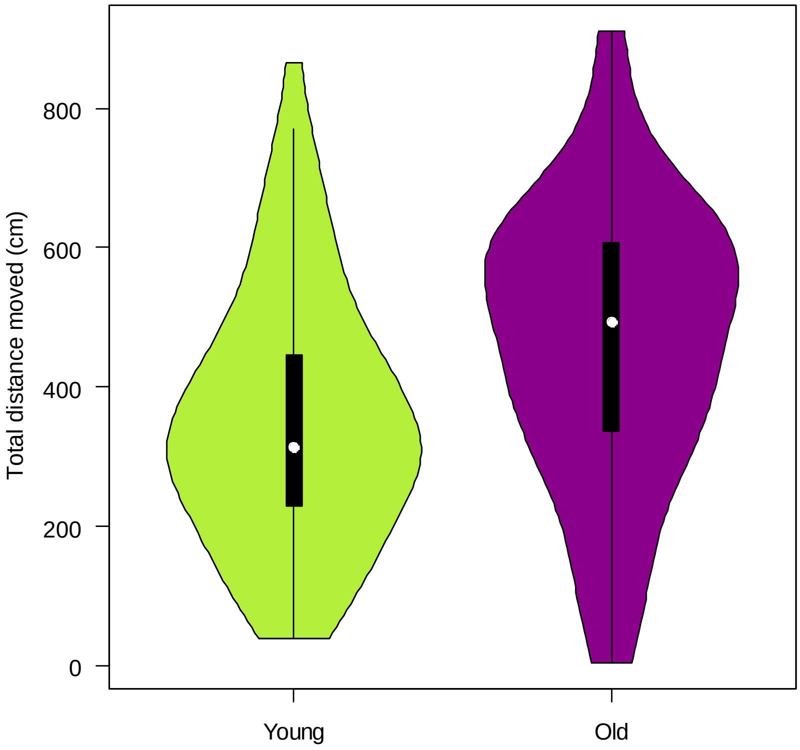
5.4. The effects of age and fungal infection on the locomotory behavior of the ant *Myrmica scabrinodis*

The high abundance of *R. wasmannii* thalli on the host cuticle (see chapter 5.1.), the absence of pathogenicity data, but the reduction in worker lifespan (see chapter 5.2.) led us to investigate in laboratory conditions whether the parasite may induce also changes in the spontaneaus locomotory behavior in the most common host ant *M. scabrinodis*. During our research we investigated if the different age cohort (old vs. young), infection status of the individuals have an effect on the locomotory behavior of *M. scabrinodis*. In order to identify the effect of other potential influencing physiological bakcground factors the fat content of the individuals was also examined as a proxy of the individual's phyisiological status.

Four behavioral parameters, one related to location (1), one to general activity (2) and three to path characteristics (3) (Bernadou and Fourcassié, 2008; Bernadou and Heinze, 2013; Bernadou *et al*., 2015 a, b). After the activity assays we examined the fat content of each individual, and we counted the number of fungal thalli from each individual.

Some studies already showed that young workers have more fat, compare to the older ones (Porter and Jorgensen, 1981; Bernadou *et al*., 2015b). Old workers had less fat than young ones based on the GLMM analysis ($z = 4.66$, $p < 0.0001$), but no differences were revealed between infected and uninfected workers in this respect ($z = 1.57$, p = NS, $n = 140$). Old individuals showed higher parasitic load, than young individuals ($z = -3.84$, $p < 0.0001$, $n = 140$).

Our results clearly showed that age displayed a significant effect on the total distance moved by individuals according the results of the LMM analysis. Old individuals moved significantly longer distances, than young individuals ($\chi^2 = 12.72$, $p < 0.0001$; Fig. 9).



Total distance moved (*cm*) by young and old individuals in the whole arena

The velocity of young individuals was lower than that of old individuals (LMM χ^2 = 9.66, p = 0.001, Fig. 10), and movement speed also increased with to increasing fat proportion (LMM χ^2 = 9.46, p = 0.002).

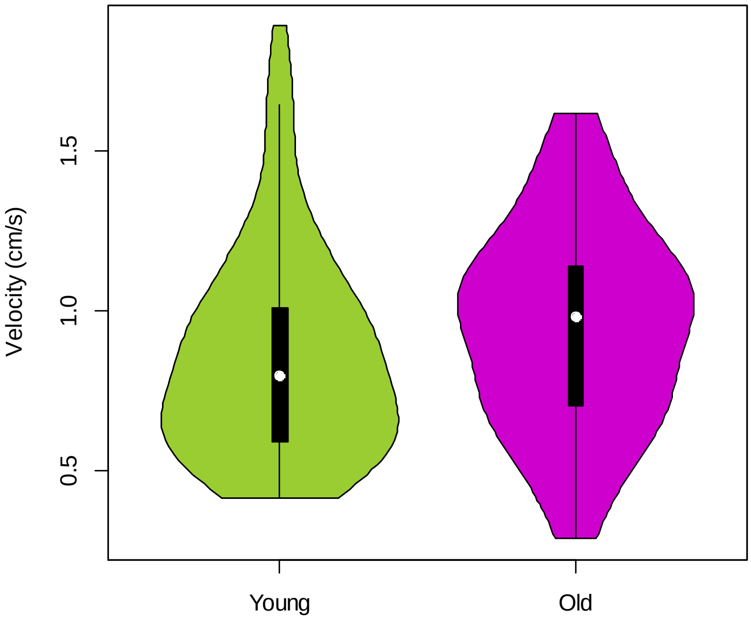


Fig. 10. The velocity (*cm/s*) of young and old individuals in the middle zone + central zone. The peripheral zone was excluded.

The fat proportion (LMM χ^2 = 12.42, p < 0.001) had significant effect on the meanderness of movement. Significant difference was also revealed between the age categories with regards to the spatial distribution of the individuals among zones: old individuals covered longer distances in the peripheral zone, than young ones (LMM χ^2 = 7.44, p = 0.006).

6. Conclusions

The principal aim of this thesis was to analzye the effect of the ectoparasitic fungus *Rickia wasmannii* on its host ant *Myrmica scabrinodis* while also studying its prevalence and distribution across different spatial scales – colonies, individuals, and body parts of individuals. The natural history of *Rickia wasmannii*, and – speaking more generally – of myrmecoparasitic Laboulbeniales fungi, is rather poorly understood compared to Laboulbeniales fungi parasitizing other insects (e.g. De Kesel, 1996).

- In the 4.1.1. chapter we reported the occurrence of five fungus species in Romania: *Aegeritella superficialis*, *Myrmicinosporidium durum*, *Pandora myrmecophaga*, *Laboulbenia camponoti* and *Rickia wasmannii* (Csata *et al*., 2013; Báthori *et al*., 2015). Our main study species was *Rickia wasmannii*, we found the fungus in 12 different locations in Romania until now. In the majority of all known cases, *M. scabrinodis* was its only or its primary host.
- In the 5.1. chapter we provided information on the prevalence and distribution of this fungus across different spatial scales – colonies, individuals, and body parts of individuals. The fungus occurred mostly in ant hosts living in more humid conditions and its within colony prevalence could reach even 100%. The high prevalence and infection intensity of *R. wasmannii* within infected colonies could be a consequence of the fungus' low virulence combined with an efficient transmission strategy.
- In the 5.2. chapter we investigated in laboratory conditions whether the parasite may induce changes in the grooming behavior of the host while also affecting its lifespan. We showed that the presence of *R. wasmannii* on the cuticle of *Myrmica scabrinodis* significantly increased the frequency and also the duration of auto- and allogrooming in infected groups.. The causes behind the decrease in lifespan in infected *M. scabrinodis* could be multiple. The fungus can reach extreme abundance on its host as presented within this thesis and thus it could cause alterations in cuticle structure or increase the risk of desiccation, but other, yet not elucidated effects could also be involved (see Kaur and Mukerji, 2006; Ortiz-Urquiza and Keyhani, 2013; Báthori *et al*., 2015).
- In the 5.3.chapter we investigated how the presence of a fungal pathogen might change the outcomes of intra- and interspecific interactions in ants. Our results emphasize that fungal infection could modify the intraspecific behavior of ants, and the presence of pathogen could significantly change the outcome of these interactions and might also influence the fitness of the host on the long.
- In the 5.4. chapter we investigated how the infections status, and the fat content of the individuals may be related to the locomotory behavior of host ants. Our findings demonstrated that the nutritional status of the individual correlated with age. In the frame of the present thesis we could demonstrate that the consequences of parasitic relationships in social context

could be manifold from changing host individual responses to potentially causing alterations in the social structure. The behavioral modifications caused by *R. wasmannii*, however, slight and not readily observable, could actually be adaptive on the part of the fungus, enabling it to reach efficiently high levels of prevalence and persistence within infected colonies.

▪ We hope that the hierarchically structured epidemiological information outlined herein may serve as a baseline for future comparative or monitoring studies, as well as contribute to a better understanding of the ecology host-parasite relationships and more specifically to that of parasitic laboulbelian fungi.

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8. Lista publicațiilor științifice ale candidatei apărute din tema tezei

1. Markó, M., Csata, E., Erős, K., Német, E., Czekes, Zs. & Rózsa, L. (2015). Distribution of the myrmecoparasitic fungus *Rickia wasmannii* (Ascomycetes: Laboulbeniales) across colonies, individuals, and body parts of *Myrmica scabrinodis*. *Journal of Invertebrate Pathology*, *submitted*, ***IF**: 2.41.*
2. Báthori, F., Csata, E. & Tartally, A. (2015). *Rickia wasmannii* increases the need for water in *Myrmica scabrinodis* (Ascomycota: Laboulbeniales; Hymenoptera: Formicidae). *Journal of Invertebrate Pathology*, 126, 78–82. ***IF**: 2.41.*
3. Csata, E. (2015). Minute mystery: ant behavioral manipulation by a fungus. Intelligens haló, 85–93.
4. Csata, E., Erős, K. & Markó, B. (2014). Effects of the ectoparasitic fungus *Rickia wasmannii* on its ant host *Myrmica scabrinodis*: changes in host mortality and

behavior. *Insectes Sociaux*, 61, 247–252. ***IF**: 1.02.*

5. Csata, E., Czekes, Zs., Erős, K., Német, E., Hughes, M., Csősz, S. & Markó, B. (2013). Comprehensive survey of Romanian myrmecoparasitic fungi: new species, biology and distribution. North-Western Journal of Zoology, 9 (1), 23–29. ***IF**: 0.747.*
6. Csata, E., (2014). Egy különleges rovarparazita gombarend: a Laboulbenia-félék (Ascomycota: Laboulbeniales). *Biologia|Acta Scientiarum Transylvanica*, 20/1, 2012.

Manuscripts in preparation

1. Csata, E., Timuş, N., Witek, M., Babik, H., Erős, K., Czekes, Zs., Rákosy, L. & Markó, B. (2015). Lockpick to the society: fungal infection facilitates the intrusion of strangers into ant colonies, *manuscript.*
2. Csata, E., Bernadou, A., Markó, B., Elena, R. T. & Heinze, J. (2015). The effects of age and fungal infection on the activity of the ant *Myrmica scabrinodis*, *manuscript.*
3. Markó, B., Schrempf, A., Csata, E. & Heinze, J. (2015). Variation in sperm length and viability in two Myrmica species with varying fungal infection potential trade offs. *manuscript.*
4. Csata, E., Molnár, D., Kötő, E.A. & Markó, B. (2015). Sanitary behaviours induced by fungal infection in *Myrmica scabrinodis, in prep.*

9. List of scientific publications not included in this thesis

1. Nédli, J., Forró, L., Csata, E., Krízsik, V., Balogh, Cs. & G-Tóth, L. (2015). Morphometric characteristics and COI haplotype diversity of Arctodiaptomus spinosus populations in sodic ponds in Hungary. *Hydrobiologia, submitted. **IF:** 2.35*
2. Csata, E., Markó, B., Erős, K., Gál, Cs., Szász-Len, A-M. & Czekes, Zs. (2012). Outstations as stable meeting points for workers from different nests in a polydomous nest system of Formica exsecta NYL. (Hymenoptera: Formicidae). Polish Journal of Ecology, 60 (1), 177–186. ***IF**: 0.506*
3. Markó, B., Czekes, Zs., Erős, K., Csata, E. & Szász-Len, A-M. (2012). The largest known polydomous system of mound building Formica ants (Hymenoptera: Formicidae) in Europe. North-Western Journal of Zoology, 8 (2), 287–291. ***IF**: 0.747*

4. Erős, K., Csata, E., Gál, Cs., Czekes, Zs., Szász-Len, A-M., Szőke, Zs., Maák, I. & Markó, B. (2011). Hangya-levéltetű-gazdanövény kapcsolatok egy egyedi szuperkoloniális rendszerben a vaslábi Fenékláp határában (Ant-aphid-host plant relationships in a unique polydomous system near the protected După Luncă area at Voșlobeni). In: Markó, B., Sárkány-Kiss, E. (ed.): A Gyergyói-medence: egy mozaikos táj természeti értékei. Presa Universitară Clujeană, Cluj-Napoca p. 244, 131–148 pp.
5. Erős, K., Markó, B., Gál, Cs., Czekes, Zs. & Csata, E. (2009). Sharing versus monopolizing: distribution of aphid sources among nests within a *Formica exsecta* Nyl. (Hymenoptera: Formicidae) supercolony. Israel Journal of Entomology, 39, 105–127.