

Against the odds of the ant competition hierarchy: submissive *Myrmica rugulosa* block access of the dominant *Lasius fuliginosus* to its aphids

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Abstract Many ant assemblages are organised in competitive hierarchies. *Myrmica rugulosa*, a submissive species at the bottom of the ant competition hierarchy, temporarily took over groups of the myrmecophilic aphid *Stomaphis quercus*, which is strictly associated with the territorial ant species *Lasius fuliginosus*. Such previously unknown intervention happened repeatedly on the nest tree of *L. fuliginosus*. Masses of *M. rugulosa* intruded into bark crevices harbouring the aphids, and blocked with their own bodies access of *L. fuliginosus* to the aphids. *Lasius fuliginosus* showed no aggression towards the intruders, but walked around and on *M. rugulosa* clusters, palpating foreign ants with their antennae. Their only countermeasure was to briefly drag or carry individual *M. rugulosa* workers that pressed themselves down and froze for the moment, and then resumed their activities. We interpret the behaviour of *M. rugulosa*, in the context of its already known interspecific relations, as a specific competitive means of existence with higher-ranked species. The behaviour—by strict definition neither interference nor exploitation competition—effectively combines submissiveness, appeasement and tenacity. We discuss similarities between such behaviour and related behaviour reported earlier in a few other

Myrmica species and *Manica rubida* while confronting physically stronger ants.

Keywords Foraging behaviour · Interspecific competition · Myrmecophile · *Stomaphis quercus* · Trophobiont

Introduction

In studies on the structuring of ant communities, interspecific competition has obtained much attention, with special emphasis on various dominance-related exclusions of subordinate species by aggressive top-dominants (for a recent review, see (Cerdá et al., 2013)). In evaluating the role of competition in community assembly of ants Vepsäläinen and Pisarski (1982), however, made the point that if competition and replacement are seen on one side of the coin, competition and coexistence reside on the other side. Coexistence by exploitative competition of submissive species is possible by shifts in daily activity or food quality (Savolainen and Vepsäläinen, 1988), or microhabitat (Savolainen and Vepsäläinen, 1989), or when single foragers locate scattered food items before aggressive, often territorial species (Reznikova, 1983), and minimise damaging physical contact by dodging away (Dlusskij, 1967; Savolainen, 1991) or by intimidating behaviour (Czechowski, 1979; Vepsäläinen and Pisarski, 1982).

In efforts to generalise competitive relations among species and the role of competition (as such a term too diffuse to have any practical use) in structuring species assemblages, context-dependent variation in interspecific relations may easily escape notion. In the following, we will describe our unique observations on *Myrmica rugulosa*, one of the lowest-ranking submissive ant species of Europe

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(Czechowski, 2004; Seifert, 2007), which occasionally took over aphid resources tended by *Lasius fuliginosus*, a competitively top-dominant species (Dlusskij, 1981). The aphid in question, the arboreal *Stomaphis quercus*, is an obligatory myrmecophilic species, trophobiotically associated with and throughout the year dependent on *L. fuliginosus* (Goidanich, 1957; Depa et al., 2012). We will use available information on similar behaviour of ants when confronted with physically or chemically dominant species, to set our observations in a more general context, and to point out still open questions for future study.

The observations

The events (recorded by KV) took place in 2013, in southernmost Finland (Sipoo, Nikkilä), in a grassy yard with a few trees, including two big birches (*Betula pendula*) growing 1.2 m apart from each other. The birches were occupied by *L. fuliginosus*, which nested between the tree roots. On the trunk of the main nest birch (ETRS-TM35FIN coordinates: N 6693934, E 404977, accuracy a couple of metres), from the ground up to over 2 m, we located in bark crevices groups of *S. quercus* aphids tended by *L. fuliginosus* (this is the first documentation of *S. quercus* in Finland). Most of the aphids were deep in the crevices, their presence only deducible from gatherings of *L. fuliginosus* workers, though part of the aphids could be located by closer examination. The birches were surrounded by a polydomous colony of *M. rugulosa*, with its numerous nest entrances in the ground dispersed within a radius of several metres.

We started observations on July 23rd after catching sight of a spectacular intrusion of *M. rugulosa* to the core of *L. fuliginosus* workers tending their aphids, and continued the observations irregularly to August 7th (later checks of the site, from August 26th onward, displayed no sign of further conflict). The intrusions by *M. rugulosa* came in waves, with varying intensity. Within the period of conflict (16 days), we visited the site at least once during 11 days, and recorded invasion by *M. rugulosa* in 7 days. Daily activity of the intrusions showed no pattern; we saw the earliest conflict before noon (then in full fling) and the last, again a strong one at 20:35. Short daily point checks may have missed earlier or later invasions, but 1 day with frequent checks from 10:30 to 19:40 revealed no *M. rugulosa* on the aphid tree (Table 1).

During the most successful intrusions, we estimated the amount of *M. rugulosa* workers on the trunk of the main nest birch of *L. fuliginosus* in one or more thousands. The intruders were concentrated in one to several clusters in and around deep bark crevices, with much lower densities on larger trunk areas. The clusters formed a dense and thick carpet of *M. rugulosa* (typically about $4 \times 10 \text{ cm}^2$ by area),

Table 1 Days and times of day when the nest trees of *Lasius fuliginosus* were checked for co-occurrence of *Myrmica rugulosa* and *L. fuliginosus*

Date	Time of day	Abundance	Location of conflict
23.7.	18:05	+++	on trunk, 0–10 cm above ground
24.7.	≈ 13:30	+++	at base and 0–10 cm above ground
25.7.	12:35	+	on ground at base of both birches
26.7.	15:10–40	++	on trunk, 0–15 cm above ground
29.7.	10:30	–	
30.7.	20:20–35	+++	at base and 0–20 cm above ground
4.8.	12:35–50	+++	on trunk, 0–10 cm above ground
	15:40	–	
5.8.	13:15–25	–	
6.8.	10:30–11.05	–	
	14:30, 15:05, 15:35	–	
	18:55, 19:40	–	
7.8.	11:25–13:05	+++	at 0–15 cm on trunk
	14:25	++	at 0–3 cm on trunk
	16:00	10–20	low at base of trunk
	16:35	6	low at base of trunk

Abundance = rough abundance estimates of *M. rugulosa*: +++ one to several thousand workers, ++ hundreds of workers, + tens of workers (numbers refer to exact amount of workers)

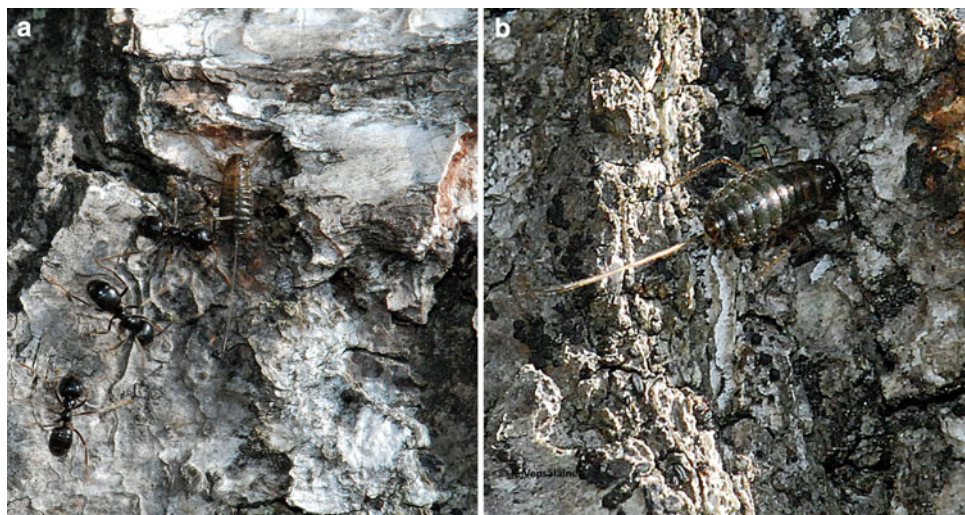
Location of conflict: always the main nest tree of *L. fuliginosus*, when conflict on trunk

with workers ranging from the surface of the bark deep into the crevices, and consequently blocking access of *L. fuliginosus* to their ‘own’ aphids (see Online Resource 1 Fig. S1). Only with lower densities or no *M. rugulosa* could some aphids be discerned in the bark crevices (see Online Resource 1 Figs. S2, S3) or occasionally to ascend the trunk (Fig. 1).

We were able to observe only once petering out of the intrusion. That day (7.8.; Table 1), thousands of *M. rugulosa* crowded on the trunk (documented for 40 min), but when checked after 80 min, their number had dropped to hundreds, and after still 1.5 h only 10–20 workers were left. Another half an hour later six *M. rugulosa* were seen on the trunk, low at the base, being carried off in the mandibles of *L. fuliginosus* workers. Our scarce behavioural data do not allow speculations on the reasons for withdrawal of *M. rugulosa* from the aphids they had temporarily reached.

Successful temporary takeovers by *M. rugulosa* of aphid gatherings in one or a few bark crevices took place at variable heights, sometimes from the ground up to 10 cm,

Fig. 1 Single *Stomaphis quercus* individuals walking up the birch trunk, followed (on photo **a**) by three workers of *L. fuliginosus*; note the long and slender trailing rostrum of the aphids. The scales of photos **a** and **b** differ (the aphids were of equal size). Photos taken on 12.9.2013 (© Kari Vepsäläinen)



sometimes twice that high (Table 1). As we were able to locate *Stomaphis* aphids in bark crevices at the height of 1.5 m, once above 2 m (the maximum reached by us standing on the ground), only a lesser part of the aphids on the trunk were ever reached by the intruders.

The *L. fuliginosus* workers, much less numerous than *M. rugulosa* at these aggregations, lingered close by or walked deliberately on the carpets of the foreign ants, palpating them with the antennae. Individual *L. fuliginosus* workers took with their mandibles an individual *M. rugulosa* worker, usually by hind leg, antenna or petiolus, dragged or carried it a few centimetres back, and then just released it. The *M. rugulosa* worker, when studied by *L. fuliginosus*, pressed itself down and froze, then underwent dragging (sometimes visibly resisting by clasping to rough surface with its feet)—after getting loose, it soon resumed attempts to move back towards the aphids. During the most hectic dragging and carrying by *L. fuliginosus*, occasionally a cluster of five to ten *M. rugulosa* workers, clasping together, tumbled down the trunk. Palpation and dragging was common behaviour by *L. fuliginosus* during less intense conflicts (and on the ground, around the nest tree), but when mass intrusions reached the aphid crevices, carrying took over (see Online Resource 2 Video S1; video legend in Online Resource 3). We noticed no sign of direct mutual or unilateral aggressiveness (either physical or chemical, e.g. use of dendrolasin by *L. fuliginosus*).

During the intrusions, part of the *M. rugulosa* workers carried a piece of grass, moss or lichen, or a birch seed—both at the feet of the birches and on the trunk. On the ground, they thus built small heaps of plant material, and on the trunk took some pieces up to the bark crevices with aphids. Whatever the intended function of the behaviour (e.g. building temporary shelters for looted aphids), searching through the heaps did not reveal anything. Not even attempts by *M. rugulosa* to drag out aphids from the

crevices were noticed. Without doubt, however, *M. rugulosa* were successful in obtaining honeydew from *Stomaphis*. This could be deduced from swollen abdomens of many workers that looked similar to those of *M. rugulosa* on maple syrup baits (placed at the site) and some odd workers coming down the trunk of a big pine close by, evidently after visiting aphids high up in the tree (uncommon behaviour by *M. rugulosa* at least in the study site).

We located nests of *M. rugulosa* around the study birch by serving pieces of oat flakes close to the birch and tracking foragers to their nest entrances. The closest nest was located 60 cm from the study birch, and six nests were found within <2 m. One forager travelled to a distance of 4.6 m before it was lost. Because we did not observe any traffic of *M. rugulosa* from or to a nest during the invasions to the study birch, we do not know the source nests of the intruders. Anyhow, the high peak numbers of workers on the aphid tree imply that workers came from more than one nest.

Discussion

Similar intimidating behaviour of *M. rugulosa* as described above has been reported to take place with *L. niger* on sugar baits and at nests (Czechowski, 1979, 1994); de Vroey 1980), and likewise inhibit physical damage by the stronger ants. The behaviour is also known in other *Myrmica* species of the *scabrinodis* group, to which *M. rugulosa* belongs (Radchenko and Elmes, 2010)—in *M. scabrinodis* with *L. niger* on baits (K. Vepsäläinen, unpubl.) and in confrontation with *Manica rubida* (Le Masne, 1967), and in *M. constricta* (originally reported as *M. rugulosa*) with *Formica sanguinea* attacking their nest (Czechowski, 2004). Generalising, the behaviour of the stronger ants includes dragging or carrying the submissive ant a few centimetres and then letting it free; the submissives freeze when

touched, dragged or carried, and after let free resume their activity (return to the bait, aphids or their nest). Also *Lepthorax* species (*L. acervorum*, *L. muscorum*) are known to effectively cut attacks by wood ants (the *Formica rufa* group) short by pressing themselves down and freezing (Vepsäläinen and Pisarski, 1982), which allows them coexistence with and indirect protection of their nests against potential competing ants (e.g. *Lasius* s. str., *Myrmica* spp., *Tetramorium caespitum*) by the wood ants (Savolainen and Vepsäläinen, 1989).

Our observations on *M. rugulosa* invading some of the aphid resources of the top-dominant *L. fuliginosus*, a species able to resist colonies of territorial wood ants (Czechowski et al., 2013), and to destroy colonies of subordinate ants, including those of *Myrmica* species (Markó et al., 2013), raise still open questions: What do our observations tell about the competition between one of the top-dominant species and the very lowest *Myrmica* species in the competitive hierarchy of ants? Why did the *L. fuliginosus* workers not use dendrolasin, their most effective means to repel even strongest alien ants, against *M. rugulosa*? What specific circumstances drove *M. rugulosa* into the seemingly exceptional intrusions to the aphids of this top-dominant species?

First, we suggest that competitive gains and losses are relative measures, and in the present case probably highly asymmetric. Even though we did not estimate methodologically adequately the sizes of the polydomous colony of *M. rugulosa* or the colony of *L. fuliginosus*, they certainly were of different orders of magnitude; probably with a workforce of several to many thousands and at least tens of thousands (perhaps some hundred of thousands), respectively. It thus seems that *M. rugulosa* successfully gained part of the alien aphid honeydew, but also that the losses to *L. fuliginosus* may have been relatively small owing to only a smaller part of the aphids exploited for only a short period of the season by the intruders—probably not a big loss to *L. fuliginosus*, but a substantial booty to *M. rugulosa*. Anyhow, it would be easier to understand the lack of physical and chemical measures by *L. fuliginosus* during the invasions that took the time and energy of quite a few of their workforce, if the intruders had used some appeasement pheromones—a topic for future research?

Second, the intrusions by *M. rugulosa* may have been caused by the long, hot and dry spells of weather, during which the vegetation at the site wilted, and perhaps killed its assumed root aphids. True, practically nothing is known about its root aphids, though some *Myrmica* species are known to associate with root aphids (Newton et al., 2011), including *M. scabrinodis* of the same species group (Depa and Wojciechowski, 2008). It is also possible that similar invasions by *M. rugulosa* are exceptional only in a statistical sense, i.e. rarely seen owing to the rarity of co-occurrence of *M. rugulosa* and *L. fuliginosus* colonies that tend

Stomaphis quercus. It should be evident, however, that we were observing only exploitation of *S. quercus* by *M. rugulosa*. Without attendance by its unique host ant, *L. fuliginosus*, the aphid colony would die out, as the colony's life cycle is dependent on host protection from egg to adult (Goidanich, 1957).

The few other above-ground exploitations of aphids by *M. rugulosa* known to us, have interesting similarities with our observations described in this note: once the tended aphid was *Stomaphis graffii* on Norway maple (*Acer platanoides*), whose eggs probably do not survive the winter if not taken care by its usual host ant, *Lasius brunneus* (Depa, 2012), and once *Aphis* sp. on *Rumex* nr. *crispus* (see Online Resource 1 Figs. S4, S5). On *Rumex*, the numerous *M. rugulosa*, when found, coexisted with a few *L. niger*, and it took several days before *L. niger* had successfully expelled *M. rugulosa* from the aphids (Czechowski, 1994). These two ant species also co-exploited *Aphis* sp. on *Tropaeolum majus* (Czechowski, 1979).

Finally, when generalising from our present observations over all known cases where the submissive *M. rugulosa* and its close relatives, and some other ants, have taken advantage of concentrated food resources (aphids, baits) by appeasement, our observations turn to an extreme variant of a more general behaviour. Usually, *Myrmica* species are known to shift to less preferred food and foraging times, and reduce aboveground foraging in presence of territorial ant species (Savolainen and Vepsäläinen, 1988, 1989), and references therein). It seems, however, that the effective appeasement behaviour of some *Myrmica* may open them access to relatively long-lasting concentrated food resources even in the presence of stronger, dominant and subdominant ant species. It is not known what triggers such intrusion of the submissive *Myrmica* to food usually monopolised by stronger ants, but extended shortage of their conventional food—or merely serendipitous opportunity—might be a sufficient trigger.

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