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Competitive pressure by territorials promotes the utilization of unusual food source by subordinate ants in temperate European woodlands

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In the presence of territorial dominant ant species, lower-ranked ants change their foraging strategy by shifting their activity in time and space and by switching to suboptimal food sources. Although important for many insect species, pollen is a rarely used food source by ants. Occasional pollen consumption was demonstrated only in a handful of ant species that are mainly lower-ranked in the competitive hierarchy. We hypothesized that the consumption of pollen by subordinate ants might be enhanced by competitive pressure exerted by dominant species. In the frame of the current study, we assessed the food preference of ant species within a supercolony of the territorial wood ant *Formica polyctena* by offering them pollen and animal protein baits. Subordinate ant species, especially *Myrmica* ants, exploited both pollen and animal protein, while *F. polyctena* foraged only for animal protein. The *Myrmica* ants exploited pollen sources more intensively on plots where *F. polyctena* dominated animal protein baits, thus interspecific competition was stronger. As suggested by our study, under suboptimal conditions, where food availability is hindered, e.g. by the presence of superior competitors, pollen can, indeed, be used as a food source by subordinate ants.

KEY WORDS: food preference, foraging, *Formica polyctena*, interspecific competition, *Myrmica*, *Temnothorax*.

INTRODUCTION

In the ant communities of temperate climate, species are hierarchically arranged, and the hierarchy consists of a few main levels of competition (see Cerdá et al. 2013 for a review). Submissive species defend only their nest territory,

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subdominant (encounter) species the food source as well, whereas dominant (territorial) species defend their whole foraging area (Pisarski & Vepsäläinen 1989). When co-occurring with territorials, subordinate species need to adapt to the strong ecological pressure exerted by the dominants. They can shift their activity in space (e.g. from the litter surface to within the litter) or in time (e.g. from daytime to evening), or they adjust their resource utilization strategy (e.g. selecting for smaller food pieces or using less rewarding sources) (Savolainen & Vepsäläinen 1989; Savolainen et al. 1989; Gallé 1990; Vepsäläinen & Savolainen 1990; Savolainen 1991; Punntilla et al. 1996; Czechowski & Vepsäläinen 2001; Czechowski & Markó 2006; Czechowski et al. 2013).

Pollen could be such an alternative resource available everywhere in the temperate climate. It is rich in nutrients, with protein levels ranging from 2.5% to 60%, but it also contains various amino acids, lipids, carbohydrates, and vitamins (Roulston & Cane 2000). While it is common in the diets of many insect groups (Wäckers et al. 2005), pollen is rarely exploited by ants (Baroni-Urbani & de Andrade 1997; Creighton 1963, 1967; Creighton & Nutting 1965; Wang & Tang 1994; Czechowski et al. 2008, 2011). For long time ants were considered to be only harmful (e.g., they consume floral nectar, deter true pollinators, cause damage to flowers) or neutral at best for pollination (see Galen & Butchart 2003; Ness 2006; de Vega et al. 2009). In addition, it is known that some plants have evolved traits to keep ants away by employing repellent scents or developed morphological features that block ants from accessing nectar (e.g. Junker et al. 2007; Junker & Blüthgen 2008; Willmer et al. 2009; Ballantyne & Willmer 2012). In recent years, though, an increasing amount of data is available on ant pollination (see Fowler & Whitford 1982; Peakall et al. 1991; Gómez et al. 1996; Puterbaugh 1998; de Vega & Gómez 2014; de Vega et al. 2014). Ants can be involved in pollination also indirectly by keeping away less efficient (smaller) pollinators thus letting more efficient (larger) ones engage (Rodríguez-Girones et al. 2013).

On the other hand, only a few ant species are known to be specialized in pollenivory (Creighton 1963, 1967), while sporadic, opportunistic pollen consumption by ants is known in a handful of tropical (Wang & Tang 1994; Cembrowski et al. 2015) and some temperate North-Palaeartic species (Czechowski et al. 2008, 2011). Czechowski et al. (2011) already hypothesized that in Northern temperate areas occasional pollenivory in ants could be promoted by seasonal food shortages caused by increasing competitive pressure from the part of territorials, as, e.g. wood ant species (subgenus *Formica* s. str.). In the frame of the present study, we tested whether variations in the presence and abundance of a territorial ant species within its polydomous system could indeed drive subordinate species to utilize pollen more frequently. A large multi-nest system of the wood ant *Formica polyctena* offered the suitable natural setup to test this hypothesis experimentally.

MATERIALS AND METHODS

Study species, site, and experimental setups

The wood ant *F. polyctena* is a widespread North-Palaeartic territorial species. Its colonies are usually highly polygynous, and owing to that, they tend to form competitively superior multi-nest systems, often containing several hundred nests (so-called supercolonies) and covering large expanses of forest. The subject of the study was a supercolony of *F. polyctena* located on the Mt Chełmowa (Chełmowa Góra; 50°53'N, 21°06'E) in the Świętokrzyski National Park, S-E Poland. The supercolony consists of ca 500 nests and stretches through all main local forest associations:

the fertile Carpathian beech forest (*Dentario glandulosae-Fagetum*), the subcontinental linden-oak-hornbeam forest (*Tilio-Carpinetum*), and the continental mixed pine forest (*Quercus roboris-Pinetum*) (see Matuszkiewicz 2007). Myrmecofauna of this region was previously studied by Rzeszowski et al. (2013).

The study site was located in the mixed pine forest area, and it included part of the *F. polyctena* supercolony with more than 40 nests (see fig. 9 in Rzeszowski et al. 2013). We selected four areas randomly within the studied part of the supercolony. In each area 15 randomly selected 20 × 20 cm observation plots were set up (N = 60) on 26 and 27 August 2013. The experiment was carried out in the peak season and period of the species activity; thus, seasonal variations in food availability or colony life cycle should not influence the outcome. The plots were located at a minimum of 10 m from a margin of any *F. polyctena* mound. We placed one item of bait in the middle of each plot. Two observation series were carried out: one with pollen bait and then one with tuna as a source of animal protein on the following day. Honeybee-collected mixed pollen pellets (~ 2 g, without any additives, purchased from apiary) were placed on 5 cm diameter round red plastic cards on bamboo sticks at flower height (~ 15 cm). On the following day, tuna flakes were put out in the same manner as pollen pellets. Tuna flakes are conventionally used as experimental animal protein bait for ants (e.g. Savolainen & Vepsäläinen 1988; Markó & Czechowski 2012; Czechowski et al. 2013). Since they are known to attract ants, they were put out 1 day after the pollen bait had been put out in order not to influence the exploitation pattern observed on the pollen bait. Thus, they served to confirm or dismiss the hypothesis that the exploitation pattern of pollen sources reflects general resource utilization patterns. Observations were carried out between 4:30 and 6 pm each day. We recorded the number and species of ants within the plots on the ground and those at the baits, separately. Data originating from plots were considered to reflect the general epigeic activity of ants including also recruitment and guarding, while data coming from bait items were considered to reflect activities strictly related to the food source exploitation. Each plot and bait was verified 4 times each day, and each observation lasted 1 min, separated from the next by 30 min in order not to disturb the bait exploitation process. Each item of bait was put out at least 15 min prior to the first observation. Subordinate ant species could be identified only to genera under field conditions in order to avoid any disturbance.

Data management

Differences in the abundance of ant species in different plots were tested using Generalized Linear Mixed Model approach (GLMM, negative binomial, maximum likelihood approximation, N = 480), separately. Plot type (based on the type of bait placed inside) was introduced as a factor. In the case of subordinate species, the abundance of the other species and its interaction with plot type were also included as covariates.

The differences in the frequency of subordinates within different plots and at different baits in the absence and in the presence of the territorial species were analyzed using Fisher's exact test, separately for every subordinate species.

Differences in the abundance of *Myrmica* individuals at different baits were compared using GLMM approach (GLMM, Poisson, maximum likelihood, N = 480). Similar analyses could not be performed for the other two species, since they were not present at both bait types in sufficient numbers (see Results). Thus, in *Myrmica*, bait type was introduced as a factor, the abundance of *F. polyctena* individuals at baits and the individuals of both species (*F. polyctena* and *Temnothorax* sp.) in plots surrounding the baits as covariates. We hypothesized that pollen consumption in *Myrmica* might be driven by high competitive pressure by *F. polyctena*. In order to test this, we performed a separate GLMM analysis (negative binomial, maximum likelihood, N = 240), where the abundance of *Myrmica* at pollen was the output variable, whereas the presence of *F. polyctena* in plots when tuna was introduced was the input variable, as a proxy of *F. polyctena*'s interest in a specific plot when something worth exploiting is present.

Changes in the abundance of *F. polyctena* at tuna baits were also analyzed (GLMM, negative binomial, maximum likelihood, $N = 240$). The abundance of *Myrmica* individuals at baits was introduced as a covariate, but also the abundance of *Myrmica* and *F. polyctena* individuals in the plots surrounding the baits. Since *Temnothorax* spp. was present in a very low number and also a low frequency at tuna baits (see Results), a similar analysis could not be performed in its case.

In all of the above models, the time sequence of observations and the plot/bait IDs were introduced as random factors in order to handle dependencies. The best models were selected with the help of automated model selection. All statistical analysis was carried out using the R 3.1.3 statistical environment (R Core Team 2018). GLMMs were performed using `glmer` and `glmer.nb` functions in `lme4` package (Bates et al. 2014), while automated model selection with the help of the `dredge` function in the `MuMIn` package (Bartoń 2013).

RESULTS

Ants in the observation plots

Three ant taxa were recorded within the plots and at the baits: *F. polyctena* was the most abundant, but ants of the genera *Myrmica* and *Temnothorax* were also quite frequent [according to Rzeszowski et al. (2013) data they were, most probably, *M. ruginodis* and *T. crassispinus*, respectively].

The abundance of the territorial *F. polyctena* was significantly higher in plots with tuna than with pollen (GLMM $z = 12.06$, $N = 480$, $P < 0.001$; Fig. 1). The best GLMM model explaining the abundance of the *Myrmica* spp. in the plots included the bait type and the abundance of *F. polyctena* and *Temnothorax* spp. individuals in the plots. The abundance of *Myrmica* spp. did not differ significantly between plots with different baits ($z = 0.55$, $P = 0.58$), while *Formica polyctena* had a negative effect on the abundance of *Myrmica* spp. ($z = -2.09$, $P < 0.05$), but on *Temnothorax* spp. did not

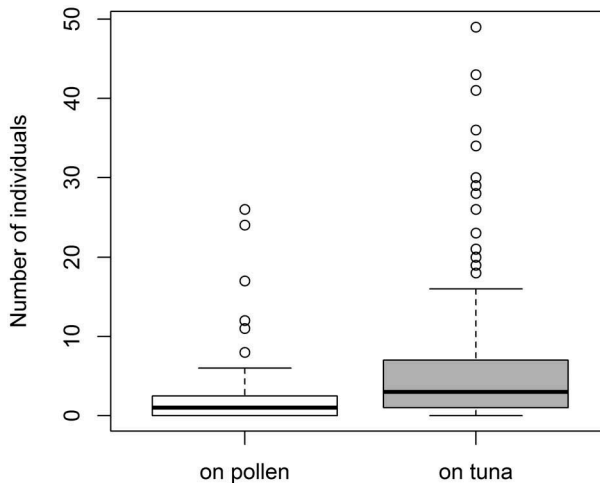


Fig. 1. — Abundance of *F. polyctena* within observation plots at baits of different types (medians, quartiles, min-max values, and outliers).

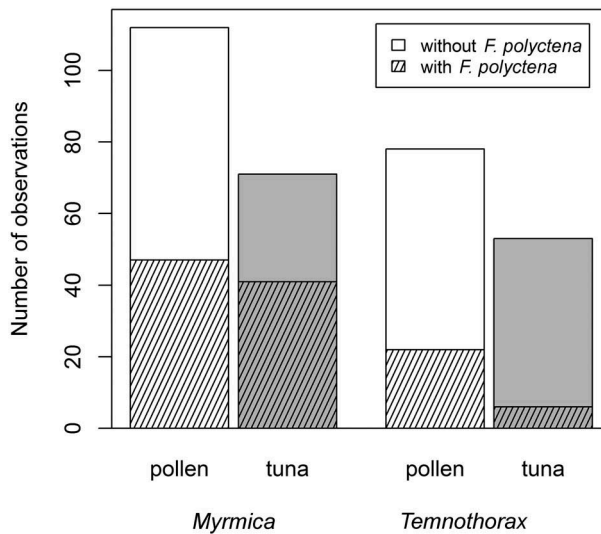


Fig. 2. — Occurrence of subordinates within observation plots at baits of different types in the absence and in the presence of *F. polyctena*.

($z = 0.36$, $P = 0.72$). The similar model in *Temnothorax* spp. included only the bait type, and its abundance was significantly lower in plots with tuna ($z = -3.39$, $P < 0.001$).

In the presence of *F. polyctena*, both subordinates occurred significantly more frequently in plots with pollen baits (Fisher's exact test $P < 0.001$, $N = 4$; Fig. 2).

Exploitation of baits

Formica polyctena individuals were heavily exploiting tuna baits, but none was recorded exploiting pollen, while *Temnothorax* individuals were rarely seen exploiting any of the baits: a single individual was recorded at pollen and three at tuna. *Myrmica* spp. was the only one to exploit both bait types.

The best model concerning the abundance of *Myrmica* individuals at both bait types contained the bait type, the abundance of *F. polyctena* at baits and those of *Myrmica* spp. in the plots. The abundance of *Myrmica* spp. was lower at tuna baits (GLMM $z = -1.99$, $N = 480$, $P < 0.05$). The abundance of *Myrmica* spp. in the plots surrounding the baits had a significant positive effect on the number of ants at baits ($z = 4.6$, $P < 0.001$), whereas the abundance of *F. polyctena* at baits had no significant effect ($z = 1.58$, $P = 0.11$). At baits with pollen, the abundance of *Myrmica* spp. was positively affected by the presence of the *F. polyctena* recorded at tuna at the same plots (GLMM $z = 3.53$, $N = 240$, $P < 0.001$).

On the other hand, the abundance of *F. polyctena* at baits with tuna was affected positively by the abundance of *F. polyctena* in the plots surrounding the baits ($z = 3.49$, $P < 0.001$), whereas the abundance of *Myrmica* spp. at baits had no effect ($z = -1.7$, $P = 0.09$). Other variables were not included.

DISCUSSION

We examined the effect of the polydomous and territorial *F. polyctena*, which represents the top dominant species of the interspecific competitive ant hierarchy in boreal and temperate Eurasia, on the utilization of alternative food sources, pollen in this specific case, by subordinate ant species. Our main result shows that subordinate species, mostly *Myrmica* spp., in the presence of stronger competitors (wood ants) forage on and recruit to pollen.

The tendency of subordinates to adapt to the presence of dominants by changing their foraging strategies, including switching to less rewarding food sources, has been documented in many different ant species (Vepsäläinen & Pisarski 1982; Savolainen & Vepsäläinen 1988; Vepsäläinen et al. 1989; Savolainen 1991; Markó & Czechowski 2012; Czechowski et al. 2013; Markó et al. 2013). One such possible alternative source could be pollen, which has a high nutritional value (Roulston & Cane 2000), but ants often avoid it, possibly because of repellents produced by plants (Willmer & Stone 1997; Ghazoul 2001; Raine et al. 2002; Wagner & Kay 2002; Nicklen & Wagner 2006; Junker et al. 2007; Junker & Blüthgen 2008; Willmer et al. 2009). Based on our findings, subordinate ant species, such as *Myrmica* spp. nesting within the territories of dominant ants, indeed tend to consume pollen, which is usually avoided or at least markedly less utilized by the stronger competitor. However, under some conditions also these species can use pollen (Czechowski & Vepsäläinen 2009; I. Maák pers. observation). Some studies on worker ant crop content demonstrated that several Palaearctic ant species, mainly those lower-ranked in the competitive hierarchy, are occasional pollen-consumers, including three *Myrmica* species: *M. schencki*, *M. rubra* and *M. ruginodis* (Czechowski et al. 2008, 2011). Moreover, pollen was found in the alimentary canal of larvae of 15 ant species from tropical forests (Cembrowski et al. 2015).

The negative effect of *F. polyctena* on subordinates is clearly revealed by its negative impact on the presence of *Myrmica* foragers at tuna. In this case, several other field studies demonstrate the decisive restrictive effects of territorial wood ants on co-occurring subordinate ant species (Vepsäläinen & Pisarski 1982; Savolainen & Vepsäläinen 1988; Vepsäläinen et al. 1989; Savolainen 1991; Markó & Czechowski 2012; Czechowski et al. 2013; Markó et al. 2013). In addition, the fact that the presence of *F. polyctena* had a negative effect on the abundance of the *Myrmica* species, but influenced positively their abundance at pollen baits implies that ants of the genus *Myrmica* in the presence of the dominant tend to switch to less rewarding food sources. Savolainen and Vepsäläinen (1989) previously demonstrated that *Myrmica* species shift their activity in space and time in the presence of *F. polyctena*. Our findings complete this picture.

It was already proven that several Palaearctic ant species occasionally consume pollen. However, our study demonstrates that the consumption of pollen in ants can be much more frequent than was originally thought, and competition can be one of the factors that promote ants to overcome the repellents produced by plants. Thus, pollen may constitute an important food source in communities where competition is fierce, and ant repellents produced by plants may play a more significant role for plants in protecting themselves against ants in ant communities with highly competitive territorials. The differential production of such repellent agents in the same plant species but under different circumstances with regards to the ant populations could be the subject of further studies.

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DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

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AUTHOR CONTRIBUTION

K. Erős, B. Markó and W. Czechowski designed the experiment, K. Erős, B. Markó, I. Maák, H. Babik, P. Ślipiński and R. Nicoară carried out the field experiments and the data collection, K. Erős, I. Maák and B. Markó carried out the data analysis. K. Erős, I. Maák, B. Markó, and W. Czechowski wrote the manuscript, and all authors participated in the revision of the final version.

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