Ant-mimicking spider actively selects its mimetic model (Araneae: Gnaphosidae; Hymenoptera: Formicidae)

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Abstract

In visual Batesian mimicry, the mimic acquires protection from predators by imitating visual signals of the model. It has not been known whether the occurrence of mimics among models is a result of selection by predators or an active choice by the mimics. Here, the occurrence of an ant-like spider, *Micaria sociabilis* KULCZYŃSKI, 1897, which occurs on tree trunks and visually imitates arboricolous *Liometopum microcephalum* (PANZER, 1798) ants, was studied. The fauna of arboricolous ant species was surveyed together with six tree characteristics in order to find which variables determined the occurrence and abundance of *M. sociabilis*. It was found that *M. sociabilis* occurred exclusively on trees where *L. microcephalum* ants occurred. The effect of any tree variable was not significant. The abundance of *M. sociabilis* increased positively with the abundance of *L. microcephalum*. Then, experiments using an olfactometer and Y-maze with volatile and contact cues obtained from the two most abundant ant species, *L. microcephalum* and *Lasius fuliginosus* (LATREILLE, 1798), were performed to find whether *Micaria* preferred any cue. *Micaria sociabilis* did not respond to volatile cues obtained from the gaster of the two ant species. In contrast, it avoided contact cues from *L. fuliginosus* and was attracted to contact cues from *L. microcephalum* ants and its gaster extract in hexane. The results thus show that *M. sociabilis* associates exclusively with *L. microcephalum* and is attracted to contact cues from this ant while avoiding cues from the competing ant. This study reveals that Batesian mimics may use kairomones to associate with visual models.

Key words: Araneae, Batesian mimicry, myrmecomorphy, pheromones.

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Introduction

Batesian mimicry is an interaction in which the mimic acquires protection from predators by imitating a low-profitable model (RUXTON & al. 2019). Batesian mimicry has been found in a variety of animals, either among closely related (e.g., species of lepidopterans, species of frogs, and species of snakes) or unrelated (e.g., hymenopterans vs spiders and flies) species (e.g., EDMUNDS 1974).

Batesian mimicry evolves in systems where a mimic co-occurs with its model. The presence of the model is essential for the predator to recall its unpalatability. There is experimental evidence showing that when the model is not present the attack rate by predators on mimics increases (e.g., PFENNIG & al. 2007). Not only the presence of the model, but also its higher abundance compared to that of the mimic is often advantageous as it also reduces the predators attack rate (LINDSTRÖM & al. 1997). For a mimic that imitates a single model species to gain a selective advantage, it is even more important to occur in the vicinity of the model so that the predator loses interest

in a closer inspection of the mimetic prey. This requires adaptations on the side of the mimic that would enable it to distinguish the model from other organisms and co-occur closely.

While morphological adaptations in Batesian mimics have frequently been studied, behavioural adaptations remain largely unexplored (RUXTON & al. 2019). Yet, the success of the mimetic phenotype relies on a combination of both these adaptations. Behavioural adaptations include active selection of the model. The importance of such behaviour, that is, the preference for a substrate, has been well documented in camouflaging species. For example, moths (KANG & al. 2012), cuttlefish (ALLEN & al. 2009), lizards (MARSHALL & al. 2016), and birds (STEVENS & al. 2017) chose backgrounds that enhanced their camouflage. An active choice should be particularly beneficial to Batesian mimics that imitate social models, such as ants. In such cases the mimic could use an intraspecific signal of the model, for example, a pheromone, to recognise it.
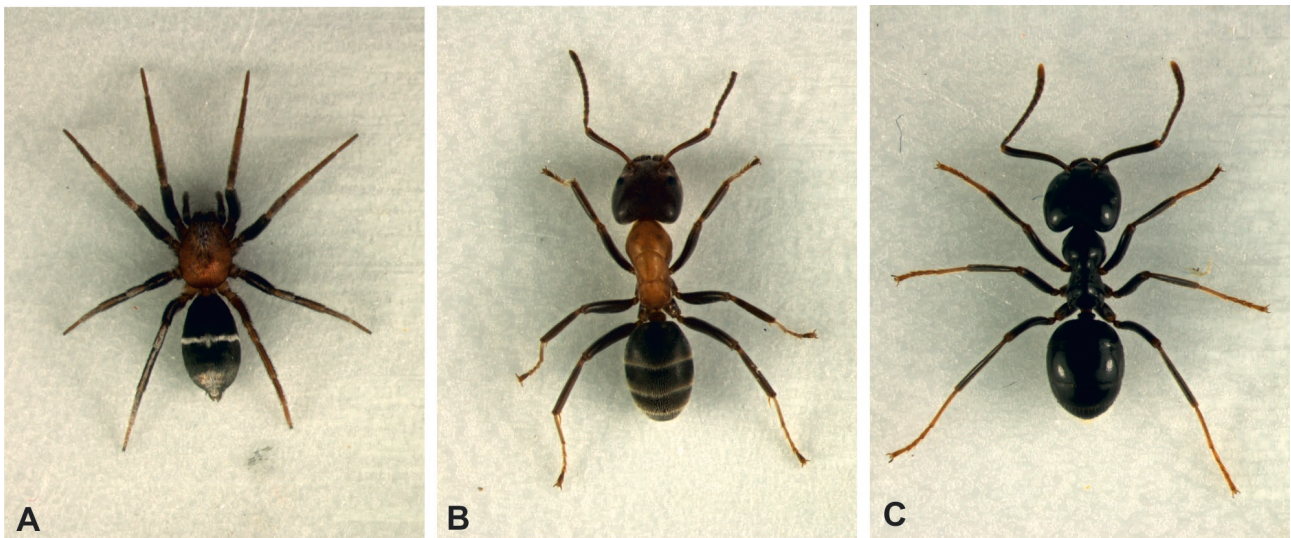
Fig. 1: Habitus of (A) *Micaria sociabilis*, (B) *Liometopum microcephalum*, and (C) *Lasius fuliginosus*.

Several ant-mimicking arthropods, such as spiders, co-occur with their ant models (CUSHING 1997). In fact, ants are the most frequent mimetic models for spiders (PEKÁR 2014). This is because ants have very similar morphology (e.g., the absence of wings), occupy similar habitats, are often superabundant compared to spider mimics, and are unpalatable for many predators (MCIVER & STONEDAHL 1993, JACKSON & NELSON 2012). The mimetic accuracy among myrmecomorphic spiders varies, with many more species being inaccurate, that is, possessing only size and colouration similarity to their models, than accurate mimics (CUSHING 2012). Such inaccurate mimics could compensate for their inaccuracy by associating more closely with their models than accurate mimics and simply, therefore, by diluting the frequency of potential attacks by predators.

Among myrmecomorphic species, *Micaria sociabilis* KULCZYŃSKI, 1897 is a very rare spider species that has so far been found only on the bark of oak trees (BOSMANS & BLICK 2000). It is a tiny species that associates with arboricolous *Liometopum microcephalum* (PANZER, 1798) ants. These ants are aggressive, polymorphic in size, and defended by communal attack (PETRÁKOVÁ & SCHLAGHAMERSKÝ 2014). *Micaria sociabilis* has frequently been observed to run among foraging ants of *L. microcephalum* (see PEKÁR & JARAB 2011a). The spider has coloration (Fig. 1) similar to this ant species (PEKÁR & JARAB 2011a). However, its overall imitation is not accurate due to the fact that it lacks body shape similarity. Nevertheless, it moves very quickly and as erratically as ants (PEKÁR & JARAB 2011a). It does not penetrate into the ant nest but hides in bark crevices.

Here, the hypothesis that *Micaria sociabilis* associates only with a single ant model, *Liometopum microcephalum*, and is able to recognise its model utilising a kairomone was tested. So, the first aim of this study was to investigate whether *M. sociabilis* co-occurs only with *Liometopum* ants, and whether any other biotic factors influence its oc-

currence. Thus, a field study was performed in which a set of potential microhabitat (tree) parameters was measured. As *M. sociabilis* was found to be associated strongly with *L. microcephalum* ants then the aim was to find by means of laboratory assays whether *M. sociabilis* recognised chemical cues (volatile or contact) from its ant model.

Methods

Field study: The study was performed in Southern Moravia, in Lednice park, where *Micaria sociabilis* has been frequently found (RŮŽIČKA 1998). There, 87 trees spread across an area of 1.27 km², were selected belonging to nine species (*Quercus robur* – 61%, *Fraxinus excelsior* – 11%, *Acer tataricum* – 11%, *Acer pseudoplatanus* – 5%, *Tilia cordata* – 5%, *Aesculus hippocastanum* – 3%, *Carpinus betulus* – 2%, *Fagus sylvatica* – 1%, *Ulmus laevis* – 1%). For each tree the following variables were recorded / measured: (1) tree species, (2) trunk diameter at breast height, (3) distance from the nearest tree, (4) per-cent of dead trunk, (5) per-cent of vegetation cover on the ground 30 cm away from the trunk, (6) per-cent of trunk without bark. In addition, on each tree, the densities of *M. sociabilis* spiders and the ant species *Liometopum microcephalum* and *Lasius fuliginosus* (LATREILLE, 1798), as well as a few other ant species (*Lasius platythorax* SEIFERT, 1991, *Camponotus* sp., *Formica* sp.), were recorded. Ants were identified using SEIFERT (1996), spiders were identified using WUNDERLICH (1979). The abundance of spiders / ants was estimated as the number of individuals seen on tree bark from the bottom of a tree to a height of 2 m during a 5 min interval. The abundance of ants was ranked as follows: 0: no ants, 1: one foraging column, 2: two-three foraging columns, 3: more than three foraging columns. The observations were made in July on a sunny day when the activity of *M. sociabilis* was highest.

The relationships between spider density and six tree variables as well as abundances of ants were modelled using non-parametric regression within a generalized

additive model with Poisson error structure (GAM-p). GAM was used because the relationship between the response variable and the predictors might not have been linear. Function gam from the mgcv package (Wood 2006) was used. Thin-plate splines were used with each continuous predictor. The non-linear predictor includes all six tree predictors. Predictors were considered significant if the p-value was less than 0.05.

Laboratory study: *Micaria sociabilis* specimens (of different stages and sex, Fig. 1A) and ants (*Liometopum microcephalum* (Fig. 1B) and *Lasius fuliginosus*, (Fig. 1C)) were collected in Lednice (South Moravia, Czech Republic) during summer by hand from the bark of oak trees. Spiders were kept in glass tubes with gypsum, moistened twice a week, and also fed twice a week with springtails reared in the laboratory. Ants from a single colony were kept in polyethylene vials (200 ml) with a wet gauze. They were maintained at approximately 23 °C and under natural L:D.

Olfactometer experiment. First, it was tested whether *Micaria sociabilis* specimens were responsive to volatile cues produced by the two most abundant ants, *Lasius fuliginosus* and *Liometopum microcephalum*. For this purpose an O-shaped olfactometer (Cárdenas & al. 2012) was used which consisted of a main chamber – a dish of diameter 6 cm and height 3 cm - into which the spider was released. The chamber was covered with a nylon mesh to allow the passage of air. The chamber had two arms (65 mm long) made of tubes 10 mm in diameter connected to two further cylindrical chambers (60 mm long, 15 mm in diameter). The chambers were made of translucent plastic material. There was a carbon filter composed of 3 g of Darco® activated carbon (granular, 12 - 20 mesh) located before the chambers to clean the air of any airborne odour. An air pump created a continuous airflow with a speed of 0.22 ± 0.1 ms^{-1} (measured by a Testo 405-V1 anemometer).

Two workers of one ant species were placed in one of the cylindrical chambers while the other remained empty. Ants were disturbed with fine pincers prior to starting the experiment. The positions of the odour source and the control were systematically switched between the two chambers. The air pump was turned on. Then, a spider was released gently into the main chamber and left for few minutes to settle down.

Thirty trials (30 spider specimens: 22 adult males, 6 adult females, 2 juveniles) were performed for each test. The main chamber with arms was cleaned with ethanol and hot water after every trial. The carbon filter was replaced every 10 trials and the used carbon was heated at 800 W in a microwave for 1.5 min in order to reactivate it. The first and the final spider choice, latency to the first choice, and the number of visits to the different arms were recorded. The experiment lasted until the spider made a final selection (i.e., when it had remained in any of the olfactometer arms for 30 seconds) or at maximum of 7 minutes.

A binomial test was used to compare the frequencies of choices against random choice (p = 0.5) for each arm

separately. The latencies for different arms were compared by means of generalized linear models with Gamma error structure and log link (GLM-g) (Pekár & Brabec 2016). The numbers of visits to arms were compared using generalized estimating equations with Poisson errors (GEE-p) from the geepack (Yan & Fine 2004) due to paired measurements (Pekár & Brabec 2018). An exchangeable correlation structure was used. Significant result was assessed at α = 0.05.

Y-maze experiment. A Y-maze frame was designed with a plastic U-shaped profile (1 cm wide and 1 cm tall), the main corridor 15 cm long and the arm corridors 12 cm long to test contact cues. The profile was covered with a glass plate. The Y-maze was used in two different experiments.

First, 10 ant workers of one species (*Lasius fuliginosus* or *Liometopum microcephalum*) were enclosed in one arm for 24 hours in order to deposit cues on the bottom. Ends of arms were blocked with a cotton. The other arm was without any ant cue and served as a control. Then, a spider was gently released at the start of the main corridor and left for 5 min to settle down. Then the arms were opened. In each trial the spider's first and final selection (i.e., when the spider had remained for at least 30 seconds in one of the arms) were recorded as well as the latency to the first choice and the number of visits to each arm. A trial was ended when *Micaria sociabilis* made its final choice. After each trial the Y-maze was washed with ethanol and hot water and then dried with paper. A total of 30 trials with *L. fuliginosus* and 30 trials with *L. microcephalum* were performed.

Second, filter paper strips soaked with different treatments were used. The strips were 35 × 15 mm in size and placed onto the bottom of one arm corridor. The control corridor contained a piece of filter paper soaked with solvent. Two solvents, hexane and dimethyl chloride, were used as it was not known whether the chemicals were polar or non-polar. The following treatments were used: (1) Gasters washed in hexane – for this purpose, 20 *Liometopum microcephalum* gasters were placed in hexane overnight in a glass 2 ml vial (N = 30); (2) Gasters washed in dimethyl chloride (as above, but with the different solvent, N = 30); (3) Gasters squeezed in hexane – 20 *L. microcephalum* gasters were placed in hexane in a 2 ml glass vial and then squeezed with a pincer (N = 43). A total of 20 μl of the solution (Feener & al. 1996) was applied on the paper strips.

In each experiment the spider's first and final choice (i.e., when the spider remained for at least 30 seconds in one of the arms) were recorded as well as the latencies and the number of visits to each arm. These data were analysed as above.

All analyses were performed using R (R Core Team 2017).

Results

Spider-ant association: The density of *Micaria sociabilis* was not affected by tree species (GAM-p, $F_7 < 0.1$,
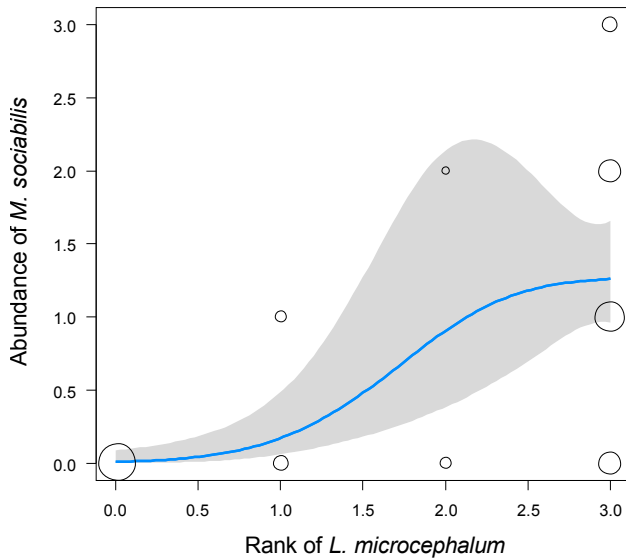
Fig. 2: Relationship between abundance of *Micaria sociabilis* and the rank density of *Liometopum microcephalum* ants per tree. The predicted non-linear model is shown (blue line) with 95% confidence band (grey area). Size of points is scaled according to their number.

P = 1.0), tree diameter (GAM-p, F_1 = 2.5, P = 0.12), distance from the nearest tree (GAM-p, F_1 < 0.1, P = 0.92), per-cent of dead trunk (GAM-p, $F_{1.4}$ = 0.2, P = 0.74), percent of vegetation cover (GAM-p, F_1 = 3.2, P = 0.08), per-cent of trunk without bark (GAM-p, $F_{1.6}$ = 0.5, P = 0.58), or abundance of *Lasius fuliginosus* (GAM-p, F_1 < 0.1, P = 0.99) or other ant species (GAM-p, F_1 = 0.6, P = 0.44). The spiders were only found on trees where *Liometopum microcephalum* ants were present: in 45% (N = 87) of trees where *L. microcephalum* ants were absent there was no *M. sociabilis* either. Abundance of *M. sociabilis* was posi-

tively (exponentially) related to the rank abundance of *L. microcephalum* ants (GAM-p, $F_{2.1}$ = 5.7, P = 0.003, Fig. 2).

Volatile cues: When exposed to *Lasius fuliginosus* volatiles, the first and final choices of *Micaria sociabilis* spiders were not significantly different from 0.5 for both arms (both Binomial tests, P > 0.1). There was no significant difference in the latency to choose between arms (GLM-g, $F_{1,28}$ <0.1, P = 0.78). Also the number of visits was not significantly different between arms (GEE-p, X^2_1 < 0.1, P = 0.78).

When exposed to *Liometopum microcephalum* volatiles the first and the final choices of *Micaria sociabilis* spiders were not significantly different between arms (Binomial test, P > 0.58). There was no significant difference in the latency to choose between arms (GLM-g, $F_{1,28}$ = 1.9, P = 0.18). Also the number of visits was not significantly different between arms (GEE-p, X^2_1 = 0.3, P = 0.56).

Contact cues: When exposed to cues of *Lasius fuliginosus* deposited on the bottom, the first and the final choices of *Micaria sociabilis* spiders were significantly different from 0.5 for both arms (both Binomial tests, P < 0.04, Fig. 3A): spiders chose the control arm more frequently. There was no significant difference in the latency to choose between arms (GLM-g, $F_{1,28}$ = 4.3, P = 0.29). The number of visits was significantly different between arms (GEE-p, X^2_1 = 12.0, P = 0.0005): there were more visits to the control arm (Fig. 3B).

When exposed to cues of *Liometopum microcephalum* deposited on the bottom, the first choice of *Micaria sociabilis* spiders was not significantly different between arms (Binomial test, P = 0.1, Fig. 3A) but the final choice was significantly different (Binomial test, P = 0.005). This time, spiders chose the arm with the ant cues more frequently. There was no significant difference in the latency to choose between arms (GLM-g, $F_{1,28}$ = 0.1, P = 0.93). The number of visits was significantly different between arms (GEE-p,
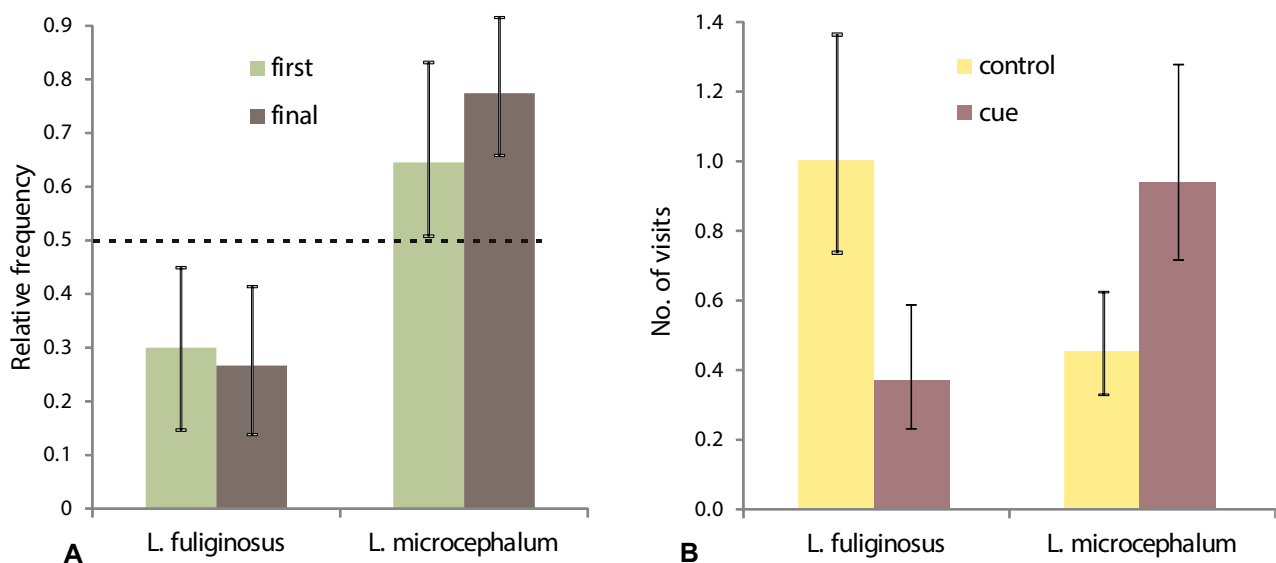

Fig. 3: (A) Comparison of the relative frequencies of the first and final choices of the arm bearing a cue of *Lasius fuliginosus* or *Liometopum microcephalum*. Horizontal dashed line shows the null hypothesis. (B) Comparison of the number of visits to the control and cue arm for *L. fuliginosus* and *L. microcephalum*. Bars are means, whiskers are 95% confidence intervals.

X^2_1 = 5.4, P = 0.02): there were more visits to the arm with cues of *L. microcephalum* (Fig. 3B).

When exposed to the hexane extract of *Liometopum microcephalum* gaster applied on a paper strip, the first and the final choices of *Micaria sociabilis* spiders were not significantly different between arms (Binomial test, P > 0.1). A similar response was observed when spiders were exposed to dimethyl chloride extract of *L. microcephalum* gaster on a paper strip (Binomial test, P > 0.36).

When, however, the gaster of *Liometopum microcephalum* was squeezed in the hexane and the mixture applied on the strip, the first choice of *Micaria sociabilis* spiders was not significantly different (Binomial test, P = 0.85) but the final choice was significantly different (Binomial test, P = 0.04). The spiders chose the arm with the ant cues more frequently (63%, N = 43). There was no significant difference in the latency to choose between arms (GLM-g, $F_{1,28}$ = 0.2, P = 0.64). The number of visits was not significantly different between arms (GEE-p, X^2_1 = 0.6, P = 0.45).

Discussion

The results of the field survey showed that none of measured tree characteristics except the occurrence and density of *Liometopum microcephalum* affected the abundance of *Micaria sociabilis* spiders. This study shows that *M. sociabilis* associates exclusively with a single ant species, as this spider species was not found on trees where *L. microcephalum* was absent. The relationship between *M. sociabilis* and *L. microcephalum* is therefore not mutualistic as the mimic relies on the presence of the model and not *vice versa*.

Micaria sociabilis does not feed on ants (PEKÁR & JARAB 2011b). It associates with ants in order to protect itself from predation. Its major predators are presumably other spiders (PEKÁR & al. 2011), *Tracheliodes* wasps (S. Pekár, unpubl.), and potentially birds. Many spiders and birds avoid ants (HÖLLDOBLER & WILSON 1990) but *Tracheliodes* wasps are specialised on *Liometopum microcephalum* ants (ZETTEL & al. 2004) and thus may catch *M. sociabilis* by mistake. The frequency of capture is probably low as our former study showed that ant-mimics are adapted to avoid predation by specialised ant-eating predators (PEKÁR & al. 2011) and models outnumber mimics.

Micaria sociabilis hunts tiny invertebrates, such as collembolans and dipterans, which hide in bark crevices where *Liometopum microcephalum* forages. Thanks to the very rough bark of oak trees, there is high spatial heterogeneity, which results in physical separation from its model. Yet, mutual encounters are frequent. *Liometopum microcephalum* is very aggressive towards *M. sociabilis*. In a former study (PEKÁR & JIROŠ 2011), we failed to find any similarity in the composition of cuticular hydrocarbons between mimics and their models which would help mimics to associate with their models. Thus, when approached, *M. sociabilis* has evolved a fast escape behaviour, by which it runs into a crevice to avoid contact with, and potential attack by its aggressive model.

Our laboratory trials revealed that *Micaria sociabilis* is attracted to chemical cues deposited by *Liometopum microcephalum* but repelled by cues deposited by *Lasius fuliginosus*. These two ant species are sympatric yet competing species in Central Europe (PETRÁKOVÁ & SCHLAGHAMERSKÝ 2011). As a result, they never co-occur in the same microhabitat, for example, tree. Given the ability of *M. sociabilis* to recognise the cues from one mimetic and one non-mimetic species, it is likely that *M. sociabilis* is also capable of identifying cues from other ant species that it does not imitate.

Since, in our study, the spiders were attracted to substrate-borne chemical cues, it is very likely that components of the trail pheromone are responsible for the attraction. Unfortunately, very little is known about the semiochemicals of *Liometopum microcephalum*. So far, only one substance, sulcatone, was identified as a defensive pheromone (GASPAR 1966, CASNATI & al. 1964). Sulcatone is a volatile component, so it must have been another compound that worked as a kairomone in this study. No trail pheromone composition of any *Liometopum* species has yet been identified. As the washing of the gaster only in hexane resulted in a positive response, the chemical substances involved must be non-polar. Some trail pheromone components are non-polar (CAMMAERTS-TRICOT & al. 1977), while others are polar (e.g., SIMON & HEFETZ 1991), so, on the basis of this information, it is not possible to predict that the extracted substances were trail pheromones. Further experiments should be performed to identify the chemicals.

The ability to recognise contact cues of a model is important not only for defence against predators. *Liometopum microcephalum* ants forage in columns on tree trunks and on the ground surrounding trees. The foraging columns shift their occurrence depending on the availability of food (PETRÁKOVÁ & SCHLAGHAMERSKÝ 2011). Therefore, *Micaria sociabilis* should be adapted to adjust its occurrence to the current presence of ants in order to decrease the likelihood of being detected by predators. *Micaria sociabilis* should use the ant kairomone also for its dispersal - to track its model whenever *L. microcephalum* disperses to new sites.

In our experiments, a mixture of ontogenetic stages and both sexes of *Micaria sociabilis* were used so it is likely that all individuals of this species use kairomones of *Liometopum micocephalum*. There could, however, be intersexual differences in the degree of receptivity if the activity of males and females differ. This is the case, for example, with camouflaging killifish, where females under predation risk showed a stronger preference for background substrate than males (KJERNSMO & MERILAITA 2012). However, as all stages and both sexes of *M. sociabilis* imitate ants and hunt prey nearby (PEKÁR & JARAB 2011b), they should be similarly adapted to recognise a kairomone of *L. microcephalum*.

The fact that *Micaria sociabilis* did not recognise volatile cues is not surprising. The ability to use volatile ant semiochemicals has been reported for ant-eating predators,

which need to locate their prey from a distance. ALLAN & al. (1996) showed that zodariid *Habronestes* spiders locate *Iridomyrmex* ants by exploiting their alarm pheromone. Another zodariid, *Zodarion rubidum* SIMON, 1914, is attracted to volatiles from the Dufour glands of Formicinae ants on which it feeds (CÁRDENAS & al. 2012). Interestingly, this spider species is also a Batesian mimic of *Lasius* ants and so uses the kairomone for two purposes. The ability to recognise cues from ants should be widespread among Batesian mimics.

It is not clear whether *Micaria sociabilis* is an inaccurate or accurate Batesian mimic. Given the fact that it is similar to its model, *Liometopum microcephalum*, only in colouration and size, it is certainly less accurate than ant-mimicking species which possess an ant-like body shape (e.g., MCIVER & STONEDAHL 1993). The body size of adult individuals of *M. sociabilis* is similar to small morphs of *L. microcephalum* workers, but juvenile individuals of *M. sociabilis* are too tiny to be similar to this ant species. It has been reported that several ant-mimicking species can perform an ontogenetic shift from one mimetic model to another (e.g., REISKIND 1970, PEKÁR & al. 2020). Juvenile individuals of *M. sociabilis* have similar colouration as adults. However, there are no other similarly coloured ants on trees; therefore, it seems that juveniles are even more inaccurate mimics. Yet, even these individuals might be protected from predation due to their low profitability. According to PENNEY & al. (2012), mimetic accuracy declines with body size because selection for accuracy is relaxed due to the decreased interest of predators.

One of the hypotheses used to explain the existence of inaccurate mimics is the multi-model hypothesis (EDMUNDS 2000), postulating that a mimic imitates several ant species of a similar phenotype. This would mean that the spider should be able to use kairomones of several ant species in order to associate with them. In this case, according to the above hypothesis, *Micaria sociabilis* should potentially be able to associate with several *Formica* species in central Europe, which exhibit phenotypic colouration similar to that of *Liometopum microcephalum*. *Formica*'s trail pheromone was not tested here, but the fact that *M. sociabilis* was not found to associate with *Formica* ants suggests that it mimics a single ant species. *Liometopum occidentale* EMERY, 1895 also exhibits a similar colouration to *L. microcephalum*; however, it occurs in the Nearctic region, where *M. sociabilis* does not occur.

I conclude that an ant-mimicking species such as *Micaria sociabilis* is adapted to actively select its model in order to enhance its protection from predators. Evidence for other myrmecomorphic species is needed to unravel whether the use of a kairomone is frequent among ant-mimics and related to mimetic accuracy.

Acknowledgements

References

ALLAN, R.A., ELGAR, M.A. & CAPON, R.J. 1996: Exploitation of an ant chemical alarm signal by the zodariid spider *Habronestes bradleyi* WALCKENAER. – Proceedings of the Royal Society B-Biological Sciences 263: 69-73.

ALLEN, J.J., MÄTHGER, L.M., BARBOSA, A., BURESCH, K.C., SOGIN, E., SCHWARTZ, J., CHUBB, C. & HANLON, R.T. 2009: Cuttlefish dynamic camouflage: responses to substrate choice and integration of multiple visual cues. – Proceedings of the Royal Society B-Biological Sciences 277: 1031-1039.

BOSMANS, R. & BLICK, T. 2000: Contribution to the knowledge of the genus *Micaria* in the West-Palaearctic region, with description of the new genus *Arboricaria* and three new species (Araneae Gnaphosidae). – Memorie della Societa Entomologica Italiana 78: 443-476.

CAMMAERTS-TRICOT, M.C., MORGAN, E.D. & TYLER, R.C. 1977: Isolation of the trail pheromone of the ant *Myrmica rubra*. – Journal of Insect Physiology 23: 421-427.

CÁRDENAS, M., JIROŠ, P. & PEKÁR, S. 2012: Selective olfactory attention of a specialised predator to intraspecific chemical signals of its prey. – Naturwissenschaften 99: 597-605.

CASNATI, G., PAVAN, M. & RICCA, A. 1964: Ricerche sul secreto delle glandole anali di *Liometopum microcephalum* Panz. – Bollettino della Societa Entomologica Italiana 94: 147-152.

CUSHING, P.E. 1997: Myrmecomorphy and myrmecophily in spiders: a review. – The Florida Entomologist 80: 165-193.

CUSHING, P.E. 2012: Spider-ant associations: an updated review of myrmecomorphy, myrmecophily, and myrmecophagy in spiders. – Psyche 2012: art. 151989.

EDMUNDS, M. 1974: Defence in animals. A survey of anti-predator defences. 1st edn. – Longman, New York, NY, 357 pp.

EDMUNDS, M. 2000: Why are there good and poor mimics? – Biological Journal of the Linnean Society 70: 459-466.

FEENER, D.H.Jr., JACOBS, L.F. & SCHMIDT, J.O. 1996: Specialized parasitoid attracted to a pheromone of ants. – Animal Behaviour 51: 61-66.

GASPAR, C. 1966: Les fourmis et l'agriculture (Hymenoptera: Formicidae). – Annales de Gembloux 72: 235-243.

HÖLLDOBLER, B. & WILSON, E.O. 1990: The ants. – Harvard University Press, Harvard, MA, 732 pp.

JACKSON, R.R. & NELSON, X.J. 2012: Specialized exploitation of ants (Hymenoptera: Formicidae) by spiders (Araneae). – Myrmecological News 17: 33-49.

KANG, C.K., MOON, J.Y., LEE, S.I. & JABLONSKI, P.G. 2012: Camouflage through an active choice of a resting spot and body orientation in moths. – Journal of Evolutionary Biology 25: 1695-1702.

KJERNSMO, K. & MERILAITA, S. 2012: Background choice as an anti-predator strategy: the roles of background matching and visual complexity in the habitat choice of the least killifish. – Proceedings of the Royal Society B-Biological Sciences 279: 4192-4198.

LINDSTRÖM, L., ALATALO, R.V. & MAPPES, J. 1997: Imperfect Batesian mimicry – the effects of the frequency and the distastefulness of the model. – Proceedings of the Royal Society B-Biological Sciences 264: 149-153.

MARSHALL, K.L., PHILPOT, K.E. & STEVENS, M. 2016: Microhabitat choice in island lizards enhances camouflage against avian predators. – Scientific Reports 6: art. 19815.

MCIVER, J.D. & STONEDAHL, G. 1993: Myrmecomorphy: morphological and behavioral mimicry of ants. – Annual Review of Entomology 38: 351-379.

PEKÁR, S. 2014: Comparative analysis of primary defences in spiders (Araneae). – Journal of Animal Ecology 83: 779-790.

PEKÁR, S. & BRABEC, M. 2016: Modern analysis of biological data. Generalized Linear Models in R. – MUNI Press, Brno, 246 pp.

PEKÁR, S. & BRABEC, M. 2018: Generalized estimating equations: A pragmatic and flexible approach to the marginal GLM modelling of correlated data in the behavioural sciences. – Ethology 124: 86-93.

PEKÁR, S., PETRÁKOVÁ DUŠÁTKOVÁ, L. & HADDAD, C.H. 2020: No ontogenetic shift in the realised trophic niche but in Batesian mimicry in an ant-eating spider. – Scientific Reports 10: art. 1250.

PEKÁR, S. & JARAB, M. 2011a: Assessment of color and behavioral resemblance to models by inaccurate myrmecomorphic spiders (Araneae). – Invertebrate Biology 130: 83-90.

PEKÁR, S. & JARAB, M. 2011b: Life-history constraints in inaccurate Batesian myrmecomorphic spiders (Araneae: Corinnidae, Gnaphosidae). – European Journal of Entomology 108: 255-260.

PEKÁR, S., JARAB, M., FROMHAGE, L. & HERBERSTEIN, M.E. 2011: Is the evolution of innacurate mimicry a result of selection by a suit of predators? A case study using myrmecomorphic spiders. – The American Naturalist 178: 124-134.

PEKÁR, S. & JIROŠ, P. 2011: Do ant-mimics imitate cuticular hydrocarbons of their models? – Animal Behaviour 82: 1193-1199.

PENNEY, H.D., HASSALL, C., SKEVINGTON, J.H., ABBOTT, K.R. & SHERRATT, T.N. 2012: A comparative analysis of the evolution of imperfect mimicry. – Nature 483: 461-464.

PETRÁKOVÁ, L. & SCHLAGHAMERSKÝ, J. 2011: Interactions between *Liometopum microcephalum* (Formicidae) and other dominant ant species of sympatric occurrence. – Community Ecology 12: 9-17.

PETRÁKOVÁ, L. & SCHLAGHAMERSKÝ, J. 2014: Worker polymorphism in the arboricolous ant *Liometopum microcephalum* (Hymenoptera: Formicidae: Dolichoderinae): Is it related to territory size? – Myrmecological News 20: 101-111.

PFENNIG, D.W., HARPER, G.R., BRUMO, A.F., HARCOMBE, W.R. & PFENNIG, K.S. 2007: Population differences in predation on Batesian mimics in allopatry with their model: selection against mimics is strongest when they are common. – Behavioral Ecology and Sociobiology 61: 505-511.

R CORE TEAM 2017: R: a language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria; <http://www.R-project.org>, retrieved on 5 April 2017.

REISKIND, J. 1970: Multiple mimetic forms in an ant-mimicking clubionid spider. – Science 169: 587-588.

RUXTON, G.D., ALLEN, W.L., SHERRATT, T.N. & SPEED, M.P. 2019: Avoiding attack: the evolutionary ecology of crypsis, aposematism, and mimicry. – Oxford University Press, Oxford, UK, 278 pp.

RŮŽIČKA, V. 1998: Spiders of southeastern Moravia. – Sborník Přírodovědného klubu v Uherském Hradišti 3: 23-35. (in Czech)

SEIFERT, B. 1996: Ameisen, beobachten, bestimmen. – Naturbuch Verlag, Augsburg, 352 pp.

SIMON, T. & HEFETZ, A. 1991: Trail-following responses of *Tapinoma simrothi* (Formicidae: Dolichoderinae) to pygidial gland extracts. – Insectes Sociaux 38: 17-25.

STEVENS, M., TROSCIANKO, J., WILSON-AGGARWAL, J.K. & SPOTTISWOODE, C.N. 2017: Improvement of individual camouflage through background choice in ground-nesting birds. – Nature Ecology and Evolution 1: 1325-1333.

WOOD, S.N. 2006: Generalized additive models: an introduction with R. – CRC Press, Boca Raton, FL, 392 pp.

WUNDERLICH, J. 1979: Revision der europäischen Arten der Gattung *Micaria* WESTRING 1851, mit Anmerkungen zu den übrigen paläarktischen Arten (Arachnida: Araneida: Gnaphosidae). – Zoologische Beiträge - Neue Folge 25: 233-341.

YAN, J. & FINE, J.P. 2004: Estimating equations for association structures. – Statistics in Medicine 23: 859-880.

ZETTEL, H., LJUBOMIROV, T., STEINER, F.M., SCHLICK-STEINER, B.C., GRABENWEGER, G. & WIESBAUER, H. 2004: The European ant hunters *Tracheliodes curvitarsis* and *T. varus* (Hymenoptera: Crabronidae): taxonomy, species discrimination, distribution, and biology. – Myrmecologische Nachrichten 6: 39-47.