

Charles University, Faculty of Science

Department of Zoology

Doctoral study programme: Zoology

Summary of the Doctoral thesis



**Spiders as senders and receivers of antipredatory warning signals
(Pavouci jako zdroje a příjemci antipredačních varovných signálů)**

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Abstract

The introductory part of this thesis sums up the state of knowledge on aposematism and mimicry, the effect of aposematic and mimetic signals on spider predators, and cases when spiders do not receive but send such signals. Attachments of the thesis include four original manuscripts. In the first study, we presented jumping spiders (*Evarcha arcuata*, Salticidae) with different colour forms (red-and-black, yellow-and-black, white-and-black) of the firebug (*Pyrrhocoris apterus*, Pyrrhocoridae). Our goal was to compare reactions of the spiders to various intensity of aposematic signalization, expecting red-and-black coloration to have the strongest effect. Aversive learning of all colour forms was equally effective, but generalization of the learned avoidance to other colour forms was more effective after switch from less (white-and-black, yellow-and-black) to more (red-and-black) conspicuously coloured prey. When tested the next day, avoidance of the white-and-black prey got mostly forgotten. In the second study, we assessed little studied sensitivity of spiders to smells of unpalatable prey. After jumping spiders learned to avoid firebugs, most of them avoided the firebug smell, showing their sensitivity not only to optical, but also to chemical part of signalization of the unpalatable prey. In the third study, we approached spiders not only as receivers, but as senders of aposematic signalization. In two species of red-and-black ladybird spiders (*Eresus kollari*, *E. moravicus*) that are considered Batesian mimics (warningly signalling, but palatable prey), we attempted to specify their model – i.e., a species protected against predators and mimicked by the spiders. The key factors were relative abundances of species similar to ladybird spiders in their localities and degree of similarity between these species and ladybird spiders based on objective criteria (colour, coloration pattern, body shape, body size). The results have shown that the most likely model of the ladybird spiders is the seven-spotted ladybird (*Coccinella septempunctata*, Coccinellidae). In the fourth study, we used jumping spiders as model predators for analysis of mimetic relationship between larvae of two true bug species, the firebug and the Mediterranean red bug (*Scantius aegyptius*, Pyrrhocoridae). The composition of the red bug's secretion notably differed from that of the firebug and was slightly less effective against spiders. Nonetheless, avoidance learning was highly effective and the aversion was well memorable in both species. The generalization was only slightly asymmetric, favouring the red bug. Mimetic relationship between the species was therefore rather Müllerian, although under specific conditions, the firebug may be put into disadvantage due to weaker defence of the red bug and slightly asymmetric generalization. Altogether, the results reveal high complexity of spider reactions towards mimetic and aposematic signals and provide support for their further use in studies of these phenomena.

1. Introduction

Aposematism and mimicry are popular cases of predator-prey interaction, being well-known even to general public. However, there are large gaps in knowledge on these topics. One of them is the role of spiders in communication by means of aposematic and mimetic signals.

Most hypotheses concerning aposematism and mimicry are tested on avian predators (Ruxton et al. 2019). Birds are important predators in nature (reviewed in Whelan et al. 2008) and their complex cognitive abilities allow testing various aposematic signals, especially visual ones. However, use of other experimental predators than birds, especially those as phylogenetically distant and neurologically different as spiders, may provide a key additional information about the functioning of aposematic and mimetic signals, especially in two aspects. Firstly, theories regarding antipredatory defence should be tested on multiple predatory taxa before being considered a general principle. Secondly, many non-avian taxa are key predators in nature, and their reactions to prey signals may reflect the actual effect of the signals on prey fitness.

As the following pages will hopefully prove, some spiders, despite having synganglions (“brains”) of a size of a pinhead (Land 2004), respond to aposematic and mimetic signals with complexity close to that observed in birds. Aside from this ability, spiders play an unenviable role of prey combining warning signals with almost no direct protection from their predators. This combination is rare in arthropods (as many insects are at least evasive or distasteful) and makes some spider taxa suitable for use in experiments concerning the effect of mimetic signals on predators.

2. Aims of the Study

The main aims of this thesis are:

- 1) Assessment of the effect of warning colouration on behaviour of jumping spiders (*Evarcha arcuata*) and comparison of the results with those previously obtained from bird predators.
- 2) Experimental study of assumed mimetic relationship between two pyrrhocorid aposematic species, *Pyrrhocoris apterus* and *Scantius aegyptius*, using jumping spiders as predators.
- 3) Testing the little known role of olfactory chemoreception in perception of aposematism by jumping spiders.
- 4) Identification of a natural model of ladybird spiders (*Eresus* spp.), warningly coloured but undefended group that probably mimics some similar, aposematic species.

3. Material and Methods

The experiments with *Evarcha arcuata* were conducted in years 2010-2015. *E. arcuata* individuals in our experiments were wild-caught, the spiders were collected in Dalejské údolí, Prague, Czech Republic. Red, natural *Pyrrhocoris apterus* larvae used in the experiments were either wild-caught individuals, or F₁ generation of wild-caught bugs. They were collected either in Dalejské údolí, Prague, Czech Republic, or in Viničná street, Prague, Czech Republic. Larvae of yellow and white colour forms of *P. apterus* were obtained from cultures obtained from Institute of Entomology, Faculty of Science, České Budějovice, Czech Republic. *Scantius aegyptius* larvae were F₁ progeny of bugs obtained in Palermo, Sicily, Italy, and Athens, Greece. Spiders and bugs were kept under standardized conditions (for details, see Raška et al. 2017). The spiders were kept in captivity for two weeks prior to the experiments, as jumping spiders have been shown to forget their feeding preferences within such period (Hill 2006). They were also not fed for one week prior to the experiments to achieve high feeding motivation in all spider individuals. Bugs were presented to the spiders individually in Petri dishes, 9 cm in diameter, which were successfully used as experimental arenas in previous experiments (Skow & Jakob 2005). In olfactory experiments (Raška et al. 2018), after spiders learned to avoid true bugs, they were presented smell of crushed true bugs (signal) and cotton (control) in Y-olfactometer. The olfactometer settings were based on those specified by Cross & Jackson (2009) and are described in detail in Raška et al. (2018).

Recordings of experiments with *E. arcuata* were analyzed using Observer XT 8.0 (Noldus Information Technology, Wageningen, Netherlands). The main explanatory variables in experiments with true bugs presented in Petri dishes were the attack rate (i.e., rate of spiders that attacked presented prey) and the capture rate (i.e., rate of spiders that killed presented prey). In experiments with Y-olfactometer, the criterion for use of the data was that the spider spent 30 seconds (standard period in such experiments, Cross & Jackson 2009) in either the signal arm or the control arm. Data from all experiments with *E. arcuata* were analyzed in up-to-date versions of R (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>).

The field part of the study of *Eresus* spp. and their potential models (Raška & Pekár 2018) was conducted in 2016-2017 in southern Moravia, Czech Republic. Once per month, relative abundances of ladybird spiders and all species potentially involved with the spiders were recorded. The up-to-date version of R (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>) was used for comparison of community structures between

consequent months. Three to five individuals of the spiders and all potential mimics that were more or equally abundant in the field were photographed using Olympus SC50 camera installed on an Olympus X12 stereomicroscope, which was lit from the anterior and posterior sides with fluorescent bulbs (13-W daylight Repti Glo 2.0 UVB) with a light spectrum similar to natural light. We took images by means of Stream Motion 1.9.4 image analysis software (Olympus Soft Imaging Solutions, 2014), which produces composite fully focused images. The photographs were analyzed using an image-processing program (Ježek 2015). Variables obtained from the program were the specimens' coloration pattern (local binary pattern, Ojala et al. 2002) and body shape (body length, body width in 40 sections evenly distributed along the body axis). After photographing, the specimens' spectral reflectance was measured using USB4000 spectrometer with a PX-2 pulsed xenon light source (Ocean Optics, Largo, FL, USA) emitting light from 220 to 750 nm.. All obtained variables were analyzed by Principal Component Analysis in two steps: (1) each variable analyzed separately, (2) PCA₁ and PCA₂ values from individual analyses used as input variables for the final analysis.

4. Results and Discussion

When repeatedly presented with different colour forms (red, yellow, white) of *Pyrrhocoris apterus* (Pyrrhocoridae) larvae, jumping spiders (*Evarcha arcuata*, Salticidae) learned to avoid all of them and prey colour had little effect. In some previous theoretical and experimental studies (reviewed in Skelhorn et al. 2016, but see Ham et al. 2006, Svádová et al. 2009), it has been suggested that the stronger the signal, the faster and more effective the avoidance-learning process should be. Our results have shown that this may not be the case in jumping spiders.

When we presented the spiders with a novel colour form after they had learned to avoid a previous one, most of them generalized learned avoidance to the novel prey. Generalization between differently-coloured prey is uncommon, as shared colour has been shown to be a principal component of mimetic signalization, especially in eyes of bird predators (Aronsson & Gamberale-Stille 2008, Rönkä et al. 2018, but see Ham et al. 2006, Svádová et al. 2009). Since spiders see their prey from closer distance than birds do, they probably focus more on other traits such as prey body shape and size, and possibly perceive non-visual aposematic signals such as vibrations and prey smell.

Although generalization was highly effective between the colour forms, it was not symmetric. Attack rates increased when the white and the yellow form were presented as a novel prey, but not when the red form was presented. Asymmetric generalization is common in birds, when similar prey differs in intensity of its signalization, be it colour (Svádová et al. 2009), colour shade (Gamberale-Stille & Tullberg 1999), or body size (Gamberale & Tullberg 1996). Moreover, during its first the novel red prey was avoided even more than the one that spider already had negative experience with. This results was caused by peak-shift (Gamberale & Tullberg 1996, Ten Cate & Rowe 2007) which made the response to a novel prey stronger due to higher intensity of its warning colour. Such reaction has already been observed in birds (Svádová et al. 2009) and its same pattern in bird and spiders suggests widespread role of peak-shift in generalization of prey avoidance.

When the bugs were presented to the spiders the day following the avoidance-learning test, all colour forms were attacked similarly, but the white one suffered from higher mortality during these attacks. This trend may be explained by go-slow theory (Guilford 1994). When a predator encounters a potentially noxious or dangerous prey, it often attacks the prey carefully. Jumping spiders have relatively short memory when it comes to learned avoidance (Hill 2006), so most of them probably had forgotten to avoid white bugs, but had only partially forgotten to avoid red and yellow bugs and had to “refresh” the avoidance.

Subsequent experiments focused on the effect of olfactory (i.e., non-contact chemical) signals of an aposematic prey (*P. apterus*) on jumping spiders (*E. arcuata*). Spiders that had learned to avoid *P. apterus* (red natural form) in training trials were put into a Y-olfactometer with two arms they could enter: one with *P. apterus* smell, one with blank control. Most spiders avoided the arm with firebug smell and entered the control one. Spider chemoreception is little known (for example, olfactory chemoreceptors have not been unambiguously specified yet, Foelix 2011) and this study was the first one to prove that spiders are able to perceive olfactory aposematic signals from their prey. A surprising secondary result was overall inactiveness of female jumping spiders in the experiments. While almost all males explored the Y-olfactometer and eventually entered one of the test arms, many females stayed motionless and their data could not be used in the analyses. Such results are surprising, considering that spider females (including jumping spiders) are considered more suitable for experimental work and males are often excluded from experiments (e.g., Nentwig 1986, Cross & Jackson 2009).

Our studies suggest that compared to females, spider males may be just as (Raška et al. 2017, submitted) or even more (Raška et al. 2018) suitable for foraging and exploratory experiments.

Nearly all spiders are predators, but they also represent a harmless and nutritious prey to other predators (Foelix 2011). We tested the hypothesis that conspicuous, red-and-black ladybird spider (*Eresus* spp., Eresidae) males protect themselves against predators by mimicking unpalatable ladybird beetles (Cloudsley-Thompson 1995). Thirty six species were found at localities of *Eresus* spp. at the time of the spiders' occurrence that resembled ladybird spiders and could serve as the spiders' models. *Coccinella septempunctata* (Coccinellidae) was abundant during the whole season at all studied sites, *Cercopis sanguinolenta* (Cercopidae) was abundant only in spring (when *E. moravicus* male occur), and *Graphosoma lineatum* (Pentatomidae) and *Hippodamia variegata* (Coccinellidae) were abundant in late summer and early autumn (when *E. kollari* occur). *Pyrrhocoris apterus*, which is a widespread red-and-black aposematic species and therefore was one of candidates for the role of the ladybird spiders' mimic, was only locally abundant at localities of *Eresus* spp. Matching phenology of a mimic and a model (i.e. occurrence at the same time, or occurrence of a mimic a little later than the model, Wallace 1867, Waldbauer et al. 1988 and references therein) and higher abundance of the model compared to the mimic (Wallace 1867, Lindström et al. 1997) are key requirements for a functional mimetic relationship, so our field data greatly limited the number of potentially effective models of *Eresus* spp.

Analyses of resemblance ladybird spiders and their models revealed that ladybird spiders are not very similar to their potential models. Such results are not surprising, considering that all potential mimics were insects, significantly differing in their body plans from the spiders. Moreover, red colouration was brighter in ladybird spiders than in their potential mimics. More intense signals of parasitic mimics compared to their models have so far been observed only in epigamic mimicry only (Kikuchi & Pfennig 2013) and this is the first record of such phenomenon in Batesian mimicry. The overall results have shown that among all sufficiently abundant mimics, *C. septempunctata* is the species most similar to ladybird spiders. The results can probably be generalized to almost whole distribution area of *Eresus* spp. (western Palaearctic region, Řezáč et al. 2008), as *C. septempunctata* is widespread in great majority of the spiders' distribution area (Nikitsky & Ukrainsky 2016, Pasqual et al. 2019).

Many true bug species possess similar red-and-black pattern (Hotová Svádová et al. 2010). Among the most similar ones are the patterns of closely related pyrrhocorids *Pyrrhocoris apterus* and *Scantius aegyptius*. Not only adults, but also larvae of these species are similar, suggesting that these species may be involved in a mimetic relationship. Analysis of larval secretion of *S. aegyptius* has revealed that although it contains chemicals typical of true bug defensive secretions (Aldrich 1988), these chemicals represent only a minor proportion of the secretion. These results suggest lower efficacy of chemical defence of *S. aegyptius* larvae compared to *P. apterus* larvae, in which the secretion is dominated by defensive chemicals (Farine et al. 1992).

Experiments using jumping spiders (*E. arcuata*) as predators have provided some support for the assumption of weaker defence in *S. aegyptius* larvae. Spiders have attacked both *P. apterus* and *S. aegyptius* during the first encounter, but *S. aegyptius* suffered from slightly higher mortality. Nonetheless, the spiders have learned to avoid both species at similar rates, and memorized the avoidance of both species until the next day similarly. The spiders' generalization of learned avoidance between both species was effective and only slightly asymmetric, favouring *S. aegyptius*. Generalization effective in both directions, protecting a newly presented true bug species against predators experienced with a similar species, makes the mimetic relationship between the species Müllerian, advantageous to both sides (Müller 1879, Sherratt 2008).

5. Conclusions

Jumping spiders are able to respond to broad spectrum of signals, such as different warning colours, body shape, or smell. Their responses are often complex enough to allow their comparison to responses of birds, the most commonly used predators in experiments testing effects of aposematic and mimetic signals. These results, along with other data obtained in recent years (e.g., Skow & Jakob 2005, Hill 2006, Taylor et al. 2014, 2015, Vickers & Taylor 2018), show that jumping spiders may serve as excellent alternative model predators for testing hypotheses concerning perception of mimetic and aposematic signals.

Many warningly coloured spiders, on the other hand, can be used as Batesian mimics in experiments with natural prey. *Eresus* spp. males may be an example of such mimics: as theoretical assumptions and preliminary experiments (Raška et al., in prep.) suggest their close-to-none antipredatory defence and Batesian mimetic relationship with co-occurring

aposematic species such as *Coccinella septempunctata*. Since the spiders' potential mimics have been specified in our study, future experimental designs may better simulate natural conditions by using a model and a Batesian mimic that are actually involved in a mimetic relationship.

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Tropek, R., Klomberg, Y., Mertens, J., Fominka, N., Kobe, I. N., Maicher, V., Padyšaková, E., Oliveira, H., Raška, J., Janeček, S.: Effects of altitude and season on the structure of pollination

networks on Mount Cameroon. The 32nd annual meeting of the Scandinavian Association of Pollination Ecologists, Blessington, 18-21 October 2018 (talk, co-author).

Raška, J., Pekár, S.: Reactions of mantises towards anti-predatory defence of *Eresus kollari* and its potential models. 31st European Congress of Arachnology, Vác, 8-13 July 2018 (talk).

Raška, J., Pekár, S.: Do ladybird spiders really mimic ladybirds? 30th European Congress of Arachnology, Nottingham, 20-25 August 2017 (talk).

Raška, J., Exnerová, A., Štys, P.: Spider perception of of aposematism and mimicry. 29th European Congress of Arachnology, Brno, 24-28 August 2015 (talk).

Raška, J., Exnerová, A., Štys, P.: Reactions of jumping spiders towards aposematic prey (Araneae, Salticidae). 28th European Congress of Arachnology, Torino, 24-29 August 2014 (talk).

Raška, J., Exnerová, A., Štys, P.: Effect of aposematism and mimicry on behaviour of spider predators. 27th European Congress of Arachnology, Ljubljana, September 2-7 2012 (poster).

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GAČR 19-09323S Mimetic complexes and evolution of inaccurate mimics, principal researcher S. Pekár (2019-2021).

GAČR P505/11/1459 Factors influencing variability in reactions of predators towards aposematic prey, principal researcher A. Exnerová (2011-2015).

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