Charles University, Faculty of Science
Department of Zoology

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Summary of the Doctoral thesis

Factors influencing effectiveness of aposematic signals against avian predators

Faktory ovlivňující efektivitu aposematických signálů vůči ptačím predátorům

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ABSTRACT

This thesis focuses on various factors affecting effectiveness of aposematic signals against avian predators. Adult, wild-caught as well as hand-reared juvenile great tits (*Parus major*) were used as predators in the experiments. The thesis consists of the following four studies.

In the first study, we compared the reactions of great tits from two geographically distant populations toward aposematic firebugs (*Pyrrhocoris apterus*) and their non-aposematic artificially made colour variant. The birds from the Bohemian population mostly avoided aposematic firebugs and attacked non-aposematic variant. Finnish birds, which lacked experience with firebugs from their natural environment, were less hesitant to attack both firebug colour forms. Although the Bohemian birds avoided the aposematic prey variant, they were not more neophobic than Finnish birds. We conclude that the geographic differences in reactions of the birds to aposematic prey can be explained by a different population-specific experience of the birds with local aposematic prey communities.

In the second study, we compared effectiveness of two chemical defence strategies in leaf beetle larvae (Chrysomela lapponica) against great tits. The birds avoided larvae devoid of external secretions after the first attack, which indicates the presence of non-volatile defensive compounds within the larval body. However, survival after the first attack was greater for larvae with intact secretions than for larvae with depleted secretions. Hence, both strategies of storage of chemicals, external secretion and storage in the body, act together against bird predation. Birds learned to avoid sequestered secretions faster compared to autogenously (*de novo*) produced secretions. Nevertheless, both strategies of chemical production provided effective protection against birds. We conclude that avian predation could contribute to the evolution of both secreted and stored defensive chemicals in *C. lapponica* larvae.

In the third study, we tested the hypothesis that different aposematic colour morphs of polymorphic leaf beetle (*Chrysomela lapponica*) differ in the effectiveness of their aposematic signals against avian predators. Juvenile great tits attacked beetles of all colour morphs (red-and-black light, red-and-black dark and metallic) at the same rate, while adults attacked light beetles at the first encounter more frequently than both dark and metallic beetles. Avoidance learning was similarly fast for all three morphs; therefore, colour displays of all morphs function as effective warning signals. Morphs differed in their memorability; the dark beetles were attacked more frequently than the other two morphs during the memory test. We hypothesise that, dark colour morphs may have a selective advantage at low population densities but they lose this advantage at high population densities due to the low memorability of their display. Thus, the direction of selective bird predation on aposematic morphs may depend on prey density, contributing to cyclic shifts in the morph frequencies.

In the fourth study, we compared the performance of great tits in sequential and simultaneous prey-discrimination tasks. Colour was more effective discriminative cue than pattern for both adult and juvenile great tits. The birds performed equally well in sequential and two-choice task, but their performance in multiple–choice task was worse than in the other two tasks. Nevertheless, these differences were found only when the birds used pattern as a cue for discrimination. The birds tested with colour, more salient cue by itself, performed equally well in all three tasks. We conclude that the type of the discrimination task may affect learning performance of bird predators, but the effect also depends on effectiveness of a particular discriminative cue; if a cue is highly salient, the type of used task might not be so important.

The results of this thesis contribute to understanding variability in reactions of avian predators toward aposematic prey as well as to understanding origin of the aposematic signal.

1 Introduction

Anti-predatory mechanisms have attracted the biologists since 19th century. One of the important strategies used by prey to protect them from predators is aposematism. The aposematic prey signals its unprofitability or unpalatability to potential predators to warn them and to prevent the attack (Mappes et al. 2005). Early detection of aposematic prey saves time and energy to a predator and increases prey survival (Sillén - Tullberg 1985a). Aposematism is considered a beneficial strategy for prey if its warning signals cause lower mortality than crypsis and it does not necessarily require complete avoidance of prey (Cott 1940).

The aposematic prey may use various traits from several sensory modalities when signalling its unprofitability to predator, nonetheless, not all traits are equally effective (Aronsson and Gamberale-Stille 2008). Most commonly known warning signals are visual displays, however acoustic, olfactory, gustatory or behavioural signals and their combinations (Ruxton et al. 2004) have also been described.

Aposematism is most widespread across insects (Lindstedt et al. 2008), but it was described in many other taxonomic groups too (Pekár 2014, Dumbacher et al. 2009). Whilst many studies have enhanced our knowledge on the phenomenon of aposematism (Ruxton et al. 2004), there are still puzzles that remain to be solved. One of the open topics is to understand when does a warning signal of aposematic prey effectively influence the response of the receiver, *i.e.,* predator. In this thesis, I evaluated the topic from the predator´s point of view; using great tits as model avian predator species, I assessed selected factors which could potentially cause variability in reactions of avian predators toward aposematic signals of prey.

2 Aims of the study

1) To test the effect of experience with local aposematic prey communities on inter-population differences in reactions of avian predators to aposematic prey.

2) To compare effectiveness of two chemical defence strategies in leaf beetle larvae (*Chrysomela lapponica*) against avian predators.

3) To test reactions of avian predators to different colour morphs of aposematic leaf beetles (*Chrysomela lapponica*).

4) To compare performance of avian predators in sequential and simultaneous prey-discrimination tasks.

3. Material and Methods

Experiments were mostly conducted in Prague (Faculty of Science, Charles University). Experiments for study 1 were also carried out in Finland (Konnevesi Research Station, University of Jyväskylä) and field experiments for study 3 were carried out in Kola Peninsula, Russia, and surroundings of Turku, Finland. Great tits (*Parus major*) were used as a model predator species in all four studies. We used both wild-caught adults and naïve, hand-reared juveniles in all studies except for the study 1, where two adult populations were tested (Bohemian and Finnish). Adult birds were captured using mist nets and housed individually under natural light and temperature conditions. The birds were allowed to habituate to the laboratory conditions for 2 - 7 days before the experiments. Juveniles were taken from nest boxes placed in Prague when 12 - 15 days old, when they were naïve with respect to any experience with unpalatable prey. Juveniles were tested after they had reached a stage of full independence (after the 35th day of life). After experiments, the birds were ringed and released in the locality of capture.

Adult firebugs (*Pyrrhocoris apterus*) used as prey species in study 1 were collected in Prague and kept under natural conditions. Two variants of firebugs were used: natural aposematic variant with red-and black pattern, and non-aposematic variant, which was obtained by painting upper parts of individuals with brown watercolour dye and chalk. Larvae of leaf beetle (*Chrysomela lapponica*) used as experimental prey in study 2 were obtained from eggs laid at the Kola Peninsula (Russia) and reared in the laboratory. Last instar of the larvae was used in the experiments. Chemically defended larvae as well as larvae devoid of secretions were tested. Furthermore, sequestered and autogenous defensive secretions per se applied onto half a mealworm painted black were tested as well. Three colour morphs (red-and-black light, red-and-black dark and metallic) of polymorphic leaf beetle (*Chrysomela lapponica*) were used as a prey species in study 3. They were reared in the laboratory from larvae collected in several localities in Russia. We used live beetles in the laboratory experiments with great tits; for field experiments, the beetles were killed by freezing. In contrast to studies 1-3, artificial prey was used in study 4; paper “bugs” baited with mealworms (*Tenebrio molitor*) soaked in either water or quinine (representing palatable and unpalatable prey respectively) with visual traits derived from real shield bug species were offered to tested birds. In studies 1, 2 and 3, the experiment consisted of a sequence of consecutive trials in which the birds were offered either a palatable control prey to check the foraging motivation, or an experimental prey. In study 4, birds were trained to discriminate between palatable and unpalatable prey presented either in sequence or simultaneously.

Each bird was tested individually and all tests were performed in experimental cages. The birds were observed through a one-way glass in the front wall of the cage. The tested prey was presented to the birds in glass Petri dishes placed on a rotating tray on the cage floor. During the multiple-choice experiments of study 4, Petri dishes with prey were attached to a plate of corrugated cardboard instead of a tray. From 2 h prior to testing, the birds were familiarized with experimental cages and deprived of food to increase their motivation to forage on prey. All experiments were video-recorded and the birds´ behaviour was continuously noted using Observer XT 8.0 (Noldus). The main variables recorded during experiments were latency to approach and attack the prey, whether the prey was attacked, killed, or eaten and duration of discomfort behaviour. In study 4, we recorded which of the two prey types was handled as the first one during two blocks of simultaneous trials present in the middle and at the end of experiments in all three types of discrimination tasks.

4. Results and Discussion

Study 1 (Exnerová et al. 2015)

The Finnish birds were expected to be more willing to attack aposematic firebugs (*Pyrrhocoris apterus*), because unlike Bohemian population, the Finnish birds lacked experience with this type of aposematic prey from their natural environment. Alternatively, the differences in behaviour toward aposematic prey could have reflected population-specific differences in exploration and neophobia (see Liebl and Martin 2014). Birds from Bohemia and from Finland did not differ in their behaviour towards non-aposematic artificially made variant of firebugs (brown); nevertheless, the differences between the two conspecific populations were found in reactions to aposematic firebugs (red). Birds from the Bohemian population mostly avoided aposematic firebugs and attacked non-aposematic variant, which confirms the results of previous studies (Exnerová et al. 2003, 2006) suggesting that the characteristic red-and-black colour pattern of firebugs facilitates their recognition by avian predators. Finnish birds were less hesitant to attack both firebug variants, and their latencies to attack both variants were correlated with the latencies to attack novel palatable prey. Bohemian birds avoided the aposematic prey, but were not more neophobic than Finnish birds. Finish birds learned to avoid both colour forms at a similar rate, which is in line with previous studies in which birds could learn to avoid aposematic prey regardless of whether its colouration was bright and conspicuous or not (Ham et al. 2006, Svádová et al. 2009).

Study 2 (Zvereva et al. 2018)

The great tits avoided larvae of the leaf beetle (*Chrysomela lapponica*) devoid of secretions after the first attack, which indicates the presence of non-volatile defensive compounds within the larval body. However, survival after the first attack was greater for larvae with intact secretions than for larvae with depleted secretions due to faster avoidance learning of avian predators and better prey memorability. The reduced survival of larvae devoid of secretions provides evidence for the higher effectiveness of volatile secretions of the larvae against avian predators. The two strategies of storage of chemicals of *C. lapponica* larvae, external secretion and storage in the body, increase prey survival through both taste rejection and enhanced avoidance learning and these two defence strategies act together against bird predation. The two storage strategies differ in the extent of costs for prey; external secretion is likely to be costlier than storing compounds internally in the body (Bowers 1992). However, our study and also findings of other studies (Skelhorn and Rowe 2006, Hotová Svádová et al. 2013) conclude that secretion of defensive chemicals of prey externally seem to be more effective for avoidance learning of avian predators compared to storage in the body. Thus, both strategies probably have similar cost-benefit ratios for prey.

We found differences between the effects of sequestered and autogenous secretions of *C. lapponica* larvae. Great tits learned to avoid sequestered secretions much faster when compared to autogenously (*de novo*) produced secretions. Also, contact with sequestered secretions elicited a stronger discomfort reaction in birds and longer initial attack latencies in the first trial. Larvae with both types of secretions survived attacks by predators at the same rate, and the birds remembered their negative experience equally well for both kinds of defences. Thus, both strategies of chemical production provided effective protection against avian predators, resulting in decreasing the possibility of attack, increasing the chance of the prey to survive the attack, or in increasing memorability of prey by predator. Another study also demonstrated that secretions sequestered from host plants are more effective against birds compared to autogenously (*de novo*) produced defences (Rowell - Rahier et al. 1995). The energetic costs for *de novo* synthesis are assumed to be higher compared to the costs for sequestration (Bowers

1992), on the other hand, other study did not find the difference between the two strategies of defence acquisition (Zvereva et al. 2017).

Study 3 (Doktorovová et al. 2019)
Naïve juvenile great tits attacked leaf beetles (*Chrysomela lapponica*) of all colour morphs (red-and-black light, red-and-black dark and metallic) at the same rate. By contrast, wild-caught tits attacked light beetles at the first encounter at the same rate as a novel control prey, but they hesitated longer before attack when presented both dark and metallic beetles. The reactions of the adult birds have likeably been influenced by their previous experience with other prey species in nature (Exnerová et al. 2015). Beetles of all colour morphs were similarly unpalatable for birds. The numbers of beetles that survived bird attack did not differ among colour morphs and almost half of the attacked beetles were released unharmed, indicating that beetle chemical defence enhances individual survival upon predator attack. The chemical defence of *C. lapponica* appeared to be mostly based on taste rejection, and on irritating rather than on toxic effects. Our findings support the conclusion by Skelhorn and Rowe (2009) that non-toxic, distasteful chemicals provide insect prey with effective protection against predators and increase the survival of individual prey through the taste-rejection behaviour by predators. Avoidance learning was similarly fast for all three leaf beetle morphs, therefore all colorations function as effective warning signals. This result is in line with previous studies (Ham et al. 2006, Svádová et al. 2009) in which birds learned to avoid new prey of different colour morphs at the same rate. Studies of bird responses to metallic (iridescent) colouration are contradictory; some have demonstrated it to be an effective aposematic signal (Fabricant et al. 2014) while other study did not (Pegram et al. 2015). Colour morphs differed in their memorability; the dark beetles were attacked more frequently than beetles of two other morphs during the memory test. Similarly, increased bird predation on more melanic individuals of wood tiger moth has been reported by Hegna et al. (2013). Our suggestion is supported by more bird approaches to the prey and longer duration of close prey inspection by the birds tested with dark beetles compared to the other two morphs, which implies that the pattern of the dark morph cannot be discriminated by birds from longer distances. Similar distance-dependent effects on birds have been demonstrated for other aposematic prey species (Gamberale-Stille et al. 2009). Experience of birds with both patterned morphs (light and dark) was not generalized to the metallic morph.

A field experiment showed that in sites with low density of *C. lapponica*, the attacks were more intensive on the light morphs than on the dark morphs, whereas in high density sites, the attack rates were similar for both morphs. Dark beetles have a survival advantage over light beetles at low *C. lapponica* population densities potentially due to the lesser conspicuousness of the dark pattern, so the frequency of the dark morph is greater at low densities compared to high density populations. Contrastingly, when the population density is high, dark beetles lose selective advantage due to the low memorability of their pattern. Thus, when the warning displays of conspecific morphs differ in their conspicuousness to birds, the direction of selective bird predation on aposematic prey morphs could change with fluctuating prey densities, leading to cyclic shifts in the morph frequencies.

Study 4 (Kuklová et al., to be submitted)
Adult great tits performed better than juveniles in the second learning test as well as in the memory test regardless of discriminative cue and task. More effective discrimination of visual cues in adults than in juveniles was also found in other avian species (Mirville et al. 2016, Franks and Thorogood 2018). Colour was more effective discriminative cue than pattern for both adult and juvenile birds. Our results are in line with previous studies showing that colour is the most salient visual discriminative cue for avian predators (Gamberale-Stille and Guilford 2003, Aronsson and Gamberale-Stille 2012). The birds tested with colour performed equally well in all three types of tasks. This suggests that if the discriminative cue is highly salient, it may not be important, which type of discrimination task is used in a particular experiment. Performance of adult birds tested with pattern as a cue was affected by type of discrimination task in the second learning test as well as memory test; birds performed worse in the multiple-choice task in comparison to other two tasks. An effect of task on performance in the second learning test was also found in juveniles tested with pattern, the birds performed worse in multiple-choice task than in two-choice task. However, juveniles did not learn successfully the pattern discrimination in any of the tasks.

Based on previous studies (Lionello and Urcuioli 1998, Beatty and Franks 2012), we predicted that the simultaneous task would be easier for the birds compared to a sequential one because of the possibility to compare the two prey items directly. Surprisingly, we have found almost no differences between sequential and two-choice task. The disadvantage of sequential task may be outweighed by higher motivation of predators to attack the prey because of higher consequences of prey rejection compared to simultaneous encounter of prey. Thus, predators may more frequently decide to taste the prey in a sequential task compared to simultaneous task and consequently learn more quickly to discriminate a prey due to more experience with it.

Contrary to our predictions, the birds performed worse in multiple-choice task than in other two tasks. Possible explanation may be limited attention of avian predators, which could lead to errors in decision making when several prey items are presented simultaneously (Dukas and Kamil 2001). Another explanation may lay in lower motivation of birds to attack the prey during multiple-choice task due to smaller cost of prey rejection compared to avoiding a single prey, which could result in gaining less experience with prey, and possibly less effective discrimination learning.

5. Conclusions

- Great tits (*Parus major*) from the Bohemian population mostly avoided aposematic firebugs (*Pyrrhocoris apterus*) and attacked non-aposematic variant. Finnish birds, which lacked experience with firebugs from their natural environment (contrastingly to Bohemian birds), were less hesitant to attack both firebug colour forms. Although the Bohemian birds avoided the aposematic prey variant, they were not more neophobic than Finnish birds. Differences between Finnish and Bohemian great tits in behaviour to aposematic variant did not correlate with the differences in exploration strategy and neophobia. We conclude that the geographic differences in reactions of the birds to aposematic prey can be explained by a different population-specific experience of the birds with local aposematic prey communities. Our findings indicate that studies on aposematism and mimicry based on geographically distant conspecific populations can be compared and generalized.

- Volatile external secretions of larvae of the leaf beetle (*Chrysomela lapponica*) provided a direct defensive effect against avian predators. Great tits also learned to avoid larvae devoid of secretions, confirming the anti-predatory function of non-volatile compounds within the larval body. However, survival after the first attack was greater for larvae with intact secretions than for larvae with depleted secretions. Hence, both strategies of storage of chemicals, external secretion and storage in the body, act together against bird predation. Secretions of *C. lapponica* larvae sequestered from host plants were more effective against avian predators than autogenously (*de novo*) produced secretions. Nevertheless, both strategies of chemical production may provide effective protection against birds. We conclude that avian predation could contribute to the evolution of both secreted and stored defensive chemicals in *C. lapponica* larvae.

- Juvenile great tits attacked all conspecific colour morphs (red-and-black light, red-and-black dark and metallic) of aposematic leaf beetles (*Chrysomela lapponica*) at the same rate, while adults attacked light beetles at first encounter more frequently than both dark and metallic beetles. The numbers of beetles that survived bird attack did not differ among morphs. Avoidance learning was similarly fast for all three morphs, hence red-and-black as well as metallic (iridescent) displays of morphs function as effective warning signals. Morphs differed in their memorability and ability to elicit generalisation in birds. We hypothesise that when aposematic signals of polymorphic prey vary in their conspicuousness for avian predators, colour morphs with less conspicuous display have a selective advantage at low population densities but they lose this advantage at high population densities due to the low memorability of their display. Thus, the direction of selective bird predation on aposematic morphs may depend on prey density, contributing to cyclic shifts in the morph frequencies.

- Colour was more effective discriminative cue than pattern for both adult and juvenile great tits. The birds performed equally well in sequential and two-choice task, but their performance in multiple–choice task was worse than in the other two tasks. However, these differences were found only when the birds used pattern as a discriminative cue. The birds tested with colour, more salient cue by itself, performed equally well in all three tasks. We conclude that the type of the discrimination task may affect the results of studies focused on discrimination learning, but the effect also depends on effectiveness of a particular discriminative cue; if a cue is highly salient, the type of used task might not be so important. Nevertheless, the type of task may affect learning performance in cases of less salient discriminative stimuli. Consequently, we hypothesise the importance of dynamics of encounters of the species engaged in mimetic complexes on the evolution of imperfect mimicry.

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Curriculum vitae

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List of publications:

to be submitted	**Kuklová, L., Jůnová, L. & Exnerová, A.** How type of task affects prey-discrimination learning in avian predators.
2019	**Doktorovová, L., Exnerová, A., Svádová, K. H., Štys, P., Adamová-Ježová, D., Zverev, V., Kozlov, M. & Zvereva, E. L**. Differential Bird Responses to Colour Morphs of an Aposematic Leaf Beetle may Affect Variation in Morph Frequencies in Polymorphic Prey Populations. *Evolutionary Biology*, 46(1), 35-46
2018	**Zvereva, E. L., Doktorovová, L., Hotová Svádová, K., Zverev, V., Štys, P., Adamová-Ježová, D., Kozlov, M. V. & Exnerová, A.** Defence strategies of *Chrysomela lapponica* (Coleoptera: Chrysomelidae) larvae: relative efficacy of secreted and stored defences against insect and avian predators. *Biological Journal of the Linnean Society*, 124(3), 533-546.
2015	**Exnerová, A., Ježová, D., Štys, P., Doktorovová, L., Rojas, B., & Mappes, J.** Different reactions to aposematic prey in 2 geographically distant populations of great tits. *Behavioral Ecology*, 26(5), 1361-1370.

Conference presentations:

2017	**Doktorovová L., Exnerová A., Jůnová L., Kišelová M., Kuncová A**.: Does type of discrimination task affect learning about prey palatability in great tits? 11th *Conference of the European Ornitologist´s union, Turku, 18.-22.8.2017* (lecture)
2015	**Doktorovová L., Jůnová L., Exnerová A.:** Effect of Experimental Design on Discrimination Learning in Great Tits (Parus major), *Behavioral ecology workshop (PhD students), Ruda Milicka, 27.-29.11.2015* (lecture)
2015	**Doktorovová L., Jůnová L., Exnerová A.:** Vplyv experimentálneho designu na diskriminačné učenie sýkorky veľkej (*Parus major*), *Konference České a Slovenské etologické společnosti 2015, České Budějovice, 4.-7.11.2015* (poster)
2015	**Doktorovová L., Jůnová L., Exnerová A.:** Vliv typu diskriminační úlohy na rychlost učení sýkory koňadry (*Parus major*), *Zoologické dny 2015, Brno, 12.-13.2. 2015* (poster)

Grants:

2019	**GAČR 19-09323S:** *Mimetic complexes and evolution of inaccurate mimics*, principal researcher S. Pekár
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Licenses and Certificates:

2017	**Course of Practical Rhetoric and Presentation** *lifelong learning – Charles University*
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