



How variation in prey aposematic signals affects avoidance learning, generalization and memory of a salticid spider



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Most studies of aposematism focus on the effect of warning signals on vertebrate predators, especially birds. In our experiments, we used jumping spiders, *Evarcha arcuata* (Araneae: Salticidae) as predators, and larvae of three colour forms (red, white, yellow) of an unpalatable firebug, *Pyrhocoris apterus* (Heteroptera: Pyrrhocoridae) as prey. The experiments were divided into four successive steps, focusing on different aspects of predator–prey interaction. (1) When presented with a firebug for the first time, the spiders captured the white, least conspicuous colour form more often than the other two. No differences in the attack latencies were observed between the colour forms. (2) In the avoidance-learning test, the spiders were offered in succession five firebugs of one of the three colour forms. The attack and capture rate decreased in all colour forms, more notably in the red, most conspicuous form. (3) After five presentations of the same prey, the spiders were presented with a different firebug colour form. The results of the generalization process were asymmetric: spiders' attack rate increased when the red prey was followed by the yellow or white one, but decreased when the red form was presented after the other colour forms. (4) Spiders attacked the same prey more often the next day, but the attacks were seldom fatal. Similarly to the initial reaction, spiders captured the white firebugs more often. Our results show that for *E. arcuata*, the red coloration can represent an effective aposematic signal. Red prey coloration decreased the attack rate during the avoidance-learning process and favoured the prey in generalization between different colour forms. Yellow coloration was moderately effective against *E. arcuata*, whereas white coloration was the least effective because of low innate bias against this signal.

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Aposematism can be defined as an association between a prey's unprofitability and a relevant signal sent by the prey to a potential predator (Mappes, Marples, & Endler, 2005). This may involve optical signals (colour, pattern, contrast, shape, etc.) as well as other modes of signalling, such as warning sounds, tastes or smells (reviewed in Komárek, 2003).

Aposematic signals usually make the prey conspicuous, which enhances the avoidance-learning process of predators (Aronsson & Gamberale-Stille, 2009; Roper & Wistow, 1986). The attacked prey may often be killed even though it is unpalatable or noxious, but the negative association made by a predator potentially protects its relatives from further attacks. Aposematism can thus be maintained by means of kin selection (Fisher, 1930). However, aposematic prey individuals may frequently survive the attack

unharmed, especially when predators sample the 'suspicious' prey (e.g. Gamberale-Stille & Guilford, 2004; Guilford, 1994; Järvi, Sillen-Tullberg, & Wiklund, 1981; Skelhorn & Rowe, 2006). The fitness of the aposematic prey can therefore be increased directly by individual selection (Järvi et al., 1981; Wiklund & Järvi, 1982).

An aposematic signal can affect the behaviour of its receiver at several levels. Even naïve predators can be affected by a signal due to the presence of an innate bias. For example, when presented with a painted novel palatable food (*Tenebrio molitor* larvae), domestic chicks, *Gallus gallus domesticus*, preferred olive and green prey items over the conspicuous (yellow, black and yellow) ones (e.g. Hauglund, Hagen, & Lampe, 2006; Schuler & Hesse, 1985).

The most prominent aspect of aposematism is that the association between signal and unprofitability can be learned by predators in a process of avoidance learning. The more salient the signal is, the easier it is for the predator to associate it with the sender's characteristics (Gamberale-Stille, Balogh, Tullberg, & Leimar, 2012; Rescorla & Wagner, 1972). This hypothesis has been supported by numerous experimental studies (reviewed in Ruxton, Sherratt, &

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Speed, 2004). Combining two or more warning signals can further increase the predator's response, as seen in experiments using optical signalling combined with acoustic or chemical cues (e.g. Marples & Roper, 1996; Rowe & Guilford, 1996).

When a predator learns to avoid a particular aposematic prey, it can generalize this experience towards a similar prey. Under some circumstances, the generalization may be asymmetric due to sensory or learning biases (ten Cate & Rowe, 2007). For example, when a predator has learned to discriminate between palatable and unpalatable prey, it may show stronger avoidance of a novel prey that differs more from the palatable one than the prey encountered during the avoidance-learning process. This phenomenon has been termed peak shift as the theoretical peak of the aversive response is shifted along the discriminative-stimulus dimension away from the original aversive stimulus (Ghirlanda & Enquist, 2003; Spence, 1937). This way predators may generalize their aversive response more effectively towards a novel prey that is more conspicuously coloured (Aronsson & Gamberale-Stille, 2008; Gamberale-Stille & Tullberg, 1999), larger (Gamberale & Tullberg, 1996a), or presented in an aggregation (Gamberale & Tullberg, 1996b).

Stronger aposematic signals may also help the learned avoidance to be remembered for longer (e.g. Guilford & Dawkins, 1991; Speed, 2000). In some experiments, conspicuous colour (Exnerová et al., 2008; but see Ham, Ihalainen, Lindström, & Mappes, 2006) or contrast against background (Alatalo & Mappes, 1996; Roper & Redston, 1987) indeed increased the maintenance of learned association in bird predators.

Most experimental data on the function of aposematic signals have been obtained from bird predators (Exnerová et al., 2008), and knowledge of how aposematism functions is especially limited for arthropod predators. However, most aposematic species are insects, and therefore are small enough to be preyed upon by other insects and spiders. Arthropod predators and parasitoids are in fact the main biotic cause of mortality of arthropod species (Symondson, Sunderland, & Greenstone, 2002) and may be crucial agents for the evolution of aposematic signals. The only two arthropod predatory taxa in which the reactions towards aposematic prey have been studied in detail are mantids (Mantodea; Berenbaum & Miliczky, 1984; Bowdish & Bultman, 1993; Prudic, Skemp, & Papaj, 2007) and jumping spiders (Araneae: Salticidae). Because of complex cognitive abilities (reviewed in Richman & Jackson, 1992), acute vision (Land, 1969; Yamashita, 1985) and tetrachromatic colour perception ranging from UV to red (Nakamura & Yamashita, 2000; Peaslee & Wilson, 1989), the jumping spiders are an excellent model for studies of the effect of aposematism.

Recently, several phenomena, first described in birds, have also been observed in jumping spiders. Jumping spiders have learned to avoid unpalatable prey (Hill, 2006; Skow & Jakob, 2006), generalized information about prey palatability to a similar prey (Taylor, Amin, Maier, Byrne, & Morehouse, 2016), and even avoided red and yellow prey without any prior experience, suggesting presence of an innate bias (Taylor, Maier, Byrne, Amin, & Morehouse, 2014). Maintenance of the learned avoidance, however, is problematic in jumping spiders: after five trials of avoidance learning, the attack rate towards unpalatable large milkweed bugs, *Oncopeltus fasciatus* (Heteroptera: Lygaeidae) on the next day increased to about 80% of that observed in naïve spiders on the previous day (Hill, 2006).

In this study, we used *Evarcha arcuata*, a common European jumping spider, as a model predator, and the third-instar larvae of (1) red-and-black, (2) yellow-and-black and (3) white-and-black colour forms of the European firebug, *Pyrrhocoris apterus*, as prey. Red-and-black, yellow-and-black and white-and-black colour combinations represent typical aposematic signals (Cott, 1940). However, the aposematic function of black-and-white coloration is context dependent (e.g. Lyytinen, Alatalo, Lindström, & Mappes,

1999; Stimson & Berman, 1990); moreover, black-and-white coloration seems to have a smaller effect on predators than the red-and-black and yellow-and-black ones (Exnerová et al., 2006; Svádová et al., 2009). We wanted to test whether the antipredator defence of the third-instar larvae of *P. apterus* is effective against jumping spiders, and how the spider's predatory behaviour is affected by the prey's colour. Specifically, we tested whether prey colour affects the degree of unlearned wariness, the process of avoidance learning and signal memorability, and how the spiders generalize between the different colour forms.

METHODS

Predators

Evarcha arcuata is a jumping spider (Araneae: Salticidae) with a Palaearctic distribution (Platnick, 2016), living in grass habitats (Buchar & Kúrka, 2001). Its body length is about 5 mm in males and 6 mm in females. It is a cursorial generalist predator feeding on other spiders and various insects, including true bugs from the family Miridae (Dobroruka, 1997; Nentwig, 1986). Jumping spiders are visually oriented and experimental studies have revealed that the species *Hasarius adansonii* could discriminate between red and yellow, red and grey, and yellow and grey colour stimuli (Nakamura & Yamashita, 2000). Although these experiments have not been performed with *E. arcuata*, we assumed that its colour perception would be similar.

Altogether we tested 200 spiders (68 males, 67 females and 65 juveniles of older instars, at least 3 mm long); each spider was tested only once. All spiders were collected in the meadows in Dalejské údolí, Prague (50°02'34.0"N, 14°21'26.1"E) between April and August 2010–2014. They were kept at 27 °C and under a natural light cycle (between 12:12 and 16:8 h light:dark) in transparent cylindrical plastic containers (70 mm tall, 30–33 mm in diameter) for at least 2 weeks before the experiments. After this period, the spiders can be considered quasinative, having forgotten all the potential prey preferences based on previous experience (Hill, 2006; Taylor et al., 2016). The spiders had access to water ad libitum and were fed twice a week with three to four micropterous fruit flies (*Drosophila melanogaster*); the number of fruit flies depended on the spiders' age and sex (adult females were fed more than males and juveniles). Each spider had been fed at least three times in captivity; the last feeding took place 1 week before the experiment to increase and standardize the foraging motivation of the spiders. We did not use females that laid eggs in captivity prior to the experiments.

Prey

We used the third-instar larvae of *P. apterus* (Heteroptera: Pyrrhocoridae) as prey. *Pyrrhocoris apterus* is a common, nearly pan-Palaearctic true bug (Kerzhner, 2001; Moulet, 1995) feeding mainly on seeds of lime trees (*Tilia cordata*, *Tilia platyphyllos*), other Malvaceae sensu stricto and black locust, *Robinia pseudacacia* (Fabaceae) (Kristenová, Exnerová, & Štys, 2011). The firebugs are mostly brachypterous and live on the ground under their host plants or upon them. The adults are about 7–12 mm long (Puchkov, 1974); the third-instar larvae are about 2–3 mm long. This size makes the third-instar larvae suitable prey for *E. arcuata*, as its highest capture rate is with prey that are 50–75% of its own size (Nentwig & Wissel, 1986). The red, wild-type firebug colour form has warning coloration (red-and-black); these colours are produced by high concentrations of red erythropterin (Bel, Porcar, Socha, Némec, & Ferre, 1997; Merlini & Nasini, 1966; Socha, 1993) and black melanin (Henke, 1924), respectively; other pteridines, such as xanthopterins and

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