



## Colour alone matters: no predator generalization among morphs of an aposematic moth

Katja Rönkä<sup>\*</sup>,<sup>1</sup>, Chiara De Pasqual<sup>1</sup>, Johanna Mappes, Swanne Gordon, Bibiana Rojas

Department of Biological and Environmental Science, University of Jyväskylä, Centre of Excellence in Biological Interactions, Finland

### ARTICLE INFO

#### Article history:

Received 12 June 2017

Initial acceptance 24 July 2017

Final acceptance 19 October 2017

MS. number: 17-00475R

#### Keywords:

learning  
polymorphism  
predator–prey interactions  
predator generalization  
warning signals  
wood tiger moth

Local warning colour polymorphism, frequently observed in aposematic organisms, is evolutionarily puzzling. This is because variation in aposematic signals is expected to be selected against due to predators' difficulties associating several signals with a given unprofitable prey. One possible explanation for the existence of such variation is predator generalization, which occurs when predators learn to avoid one form and consequently avoid other sufficiently similar forms, relaxing selection for monomorphic signals. We tested this hypothesis by exposing the three different colour morphs of the aposematic wood tiger moth, *Arctia plantaginis*, existing in Finland to local wild-caught predators (blue tits, *Cyanistes caeruleus*). We designed artificial moths that varied only in their hindwing coloration (white, yellow and red) keeping other traits (e.g. wing pattern and size) constant. Thus, if the birds transferred their aversion of one morph to the other two we could infer that their visual appearances are sufficiently similar for predator generalization to take place. We found that, surprisingly, birds showed no preference or aversion for any of the three morphs presented. During the avoidance learning trials, birds learned to avoid the red morph considerably faster than the white or yellow morphs, confirming previous findings on the efficacy of red as a warning signal that facilitates predator learning. Birds did not generalize their learned avoidance of one colour morph to the other two morphs, suggesting that they pay more attention to conspicuous wing coloration than other traits. Our results are in accordance with previous findings that coloration plays a key role during avoidance learning and generalization, which has important implications for the evolution of mimicry. We conclude that, in the case of wood tiger moths, predator generalization is unlikely to explain the unexpected coexistence of different morphs.

© 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Aposematic organisms display warning signals that predators learn to associate with their unprofitability (Poulton, 1890). The survival of such prey is thus highly dependent on a predator's ability to learn, remember and generalize their learned avoidance to other individuals sharing the same warning signal (reviewed in Ruxton, Sherratt, & Speed, 2004). Signal sharing among aposematic prey benefits both the prey and their potential predators: (1) a given individual has a lower risk of predation when more individuals share the same warning signal, and (2) predators benefit from not having to sample as many unprofitable or toxic prey and can more easily remember one and not multiple signals (ten Cate & Rowe, 2007; Ghirlanda & Enquist, 2003; Guilford & Dawkins, 1991; Müller, 1878; Rowland, Ihalainen, Lindström, Mappes, & Speed,

2007). Therefore, local polymorphism in warning coloration is expected to be selected against (Chouteau, Arias, & Joron, 2016; Endler, 1991; Joron & Mallet, 1998; Lindström, Alatalo, Lyytinen, & Mappes, 2001; Mallet & Barton, 1989; Mallet & Joron, 1999; but see also Ihalainen, Lindström, & Mappes, 2007 who found no evidence for slower avoidance learning of single versus multiple signals).

Despite the predicted disadvantages, warning signal polymorphisms are present in several aposematic taxa, such as frogs (Amézquita, Castro, Arias, González, & Esquivel, 2013; Rojas & Endler, 2013), ladybirds (O'Donald & Majerus, 1984; Průchová, Nedvěd, Veselý, Ernestová, & Fuchs, 2014) and butterflies (Jiggins & McMillan, 1997). In fact, they seem to be more common than expected considering that warning signals are predicted to be under positive frequency-dependent selection (Müller, 1878; Ruxton et al., 2004). One possible explanation for the co-occurrence of several warning signal forms within the same population is predator generalization. This refers to a predator's ability to transfer its learned avoidance of one signal to other signal(s) that share

\* Correspondence: K. Rönkä, Department of Biological and Environmental Science, University of Jyväskylä, Centre of Excellence in Biological Interactions, P.O. Box 35, FI-40014, University of Jyväskylä, Finland.

E-mail address: [katja.h.ronka@jyu.fi](mailto:katja.h.ronka@jyu.fi) (K. Rönkä).

<sup>1</sup> Shared first authorship.

common characteristics (Gamberale-Stille & Tullberg, 1999; Guilford & Dawkins, 1991; Lindström, Alatalo, Mappes, Riipi, & Vertainen, 1999; Mappes & Alatalo, 1997). Generalization can be symmetric, meaning that once one colour is learned it is equally possible to transfer the learned aversion to other similar colours, or asymmetric, implying that transferring a learned avoidance from one colour to other(s) depends on the signal salience (Aronsson & Gamberale-Stille, 2008; Exnerová et al., 2006; Gamberale & Tullberg, 1996; Gamberale-Stille & Tullberg, 1999; Ham, Ihalainen, Lindström, & Mappes, 2006; Ruxton, Franks, Balogh, & Leimar, 2008; Waldron et al., 2017).

Predator learning involves different cognitive processes that establish the association between warning coloration and unprofitability, and aid the memorization of this association once established. This learning process may vary between predators even at intraspecific levels (e.g. Adamová-Ježová, Hospodková, Fuchsová, Štys, & Exnerová, 2016; Endler & Mappes, 2004; Exnerová et al., 2015; Exnerová, Svádová, Fučíková, Drent, & Štys, 2010; Karlíková, Veselý, Beránková, & Fuchs, 2016; Lindström, Alatalo, & Mappes, 1999; Sherratt & Macdougall, 1995; Skelhorn, Halpin, & Rowe, 2016). Predators may also vary in their ability to cope with defended prey, due for example to dietary conservatism (Marples & Kelly, 1999; Mettke-Hofmann, Winkler, & Leisler, 2002; Turini, Veselý, & Fuchs, 2016; Webster & Lefebvre, 2000). Therefore, investigating how predators learn to associate the appearance of prey with the noxious effects of their unprofitability is crucial to understanding how signal variation can be maintained within a population. During the learning process predators acquire information about the nutrient and toxin content of aposematic prey. Thus, individual predators are expected to make different decisions on how to use the information gathered from an encounter with aposematic prey (Exnerová et al., 2003, 2007; Halpin, Skelhorn, & Rowe, 2014; Lynn, 2005; Skelhorn et al., 2016; Trimmer et al., 2011), and modify their ingestion of toxic prey according to their toxic burden (Skelhorn & Rowe, 2007).

Generalized avoidance should be broad and persist for a relatively long time to offer protection to different warningly coloured prey morphs. On the other hand, naïve predators can also avoid warningly coloured prey due to innate wariness, neophobia or dietary conservatism (Exnerová et al., 2007; Lindström et al., 1999; Marples & Kelly, 1999; Marples & Mappes, 2011), which could be further reinforced by the short-term effects of negative experience with other aposematic prey. It has been suggested that multiple modalities of warning signals can help predators discriminate between palatable and unpalatable prey (Kazemi, Gamberale-Stille, & Leimar, 2015; Siddall & Marples, 2008). However, generalized avoidance of aposematic prey can also be based on cues of different sensory modalities, such as odour, sound, colour or pattern or combinations of these. Depending on the cognitive processes of predators, they could also associate their negative experience with certain stimuli to any other stimuli encountered simultaneously (Mackintosh, 1975; Pavlov, 1927). These results emphasize the importance of studying how multiple cues and separate signal components influence a predator's decision to attack prey (Kikuchi, Mappes, Sherratt, & Valkonen, 2016; Rowe & Halpin, 2013).

Here, we tested the hypothesis that the hindwing colour polymorphism of an aposematic moth is enabled by predator generalization, and investigated whether or not that generalization is symmetric. We exposed paper models of the different hindwing colour morphs of the wood tiger moth, *Arctia plantaginis* (formerly known as *Parasemia plantaginis*, Rönkä, Mappes, Kaila, & Wahlberg, 2016) to natural predators (blue tits, *Cyanistes caeruleus*), and examined whether, once they learned to avoid one of the colour morphs, they would generalize this aversion to the two unlearned colour morphs, which would allow multiple morphs to coexist. A

lack of generalization among colour morphs would mean that birds pay more attention to colours than to other cues of the moth wings.

## METHODS

The wood tiger moth is an aposematic diurnal moth with a Holarctic distribution (Hegna, Galarza, & Mappes, 2015). They have two different chemical defences, one of which is secreted from the prothoracic glands. Although the chemical composition is not fully known, these fluids contain two types of methoxy-pyrazines, which are produced de novo (Burdfield-Steel, Pakkanen, Rojas, Galarza, & Mappes, 2016) and make them a deterrent to birds. Experiments with bird predators suggest that the fluids of yellow males have a more repulsive odour (Rojas et al., 2017), while those of white males taste worse (Rojas, Burdfield-Steel & Mappes, 2015). Individuals vary in the degree of melanization and black patterning of the wings, as well as in levels of chemical defence, but the most striking feature of the wood tiger moth is its local hindwing colour polymorphism (Hegna et al., 2015). In Europe, its forewings present a black and white pattern in both males and females, whereas the hindwing colour combined with black pattern differs between the sexes (e.g. Galarza, Nokelainen, Ashrafi, Hegna, & Mappes, 2014; Hegna & Mappes, 2014). The distinct white and yellow male morphs are genetically determined by one autosomal locus and at least three alleles, dominant white, recessive white and intermediate yellow (Galarza, Nokelainen, & Mappes, 2016), while female hindwing coloration varies continuously from yellow to red (Lindstedt, Schroderus, Lindström, Mappes, & Mappes, 2016; Fig. 1). In Finland, for example, yellow and white males may occur within one population (Nokelainen, Valkonen, Lindstedt, & Mappes, 2014) whereas female hindwing coloration is mostly red (Hegna et al., 2015).

To study the reaction of bird predators (see below for details on procedure) to the different hindwing colour morphs, we used artificial moth models. The usage of artificial prey allows for the controlled manipulation of one or more warning signal components at a time, while accounting for how predators (i.e. birds) would see them (Endler & Mielke, 2005). In this way, other components can be kept constant and independent of prey qualities, such as the variation in the level of chemical defence or behaviour (Karlíková et al., 2016; Lindström, Alatalo et al., 1999; Veselý & Fuchs, 2009). Here, our artificial moth models eliminated individual variation in moth size, shape, degree of melanization, wing pattern, wing posture, behaviour, smell or taste. Model wings were constructed with the software GIMP (2.8.16; <http://www.gimp.org/>) from pictures of a real male wood tiger moth specimen collected in Finland. Pictures of one forewing and one hindwing of a typical white moth were duplicated to obtain a symmetric pattern for the whole model. The melanization pattern of the moths used was a representative sample of a wing pattern in Finland (Fig. 1). To control for the amount and shape of melanized (mainly black) pattern of the wings, yellow and red models were created from the same wing picture, changing the hue of the white parts of the hindwing towards yellow or red. Finished models were printed double sided (HP Color LaserJet CP2025) on waterproof (Rite In The Rain, Tacoma, WA, U.S.A.) paper. To ensure that the model colours resembled the real wood tiger moth morphs, colour reflectance was measured with an Ocean Optics Maya2000 Pro spectrometer and average reflectance curves from three spots in the model hindwing coloration were compared to average reflectance curves of white, yellow and red moth hindwings (Fig. 1). Models were then cut out from the paper and completed with a body made of rolled pastry, composed of two parts of lard, six parts of coarse wheat flour and one part of water to make them edible. The total

Download English Version:

<https://daneshyari.com/en/article/8488735>

Download Persian Version:

<https://daneshyari.com/article/8488735>

[Daneshyari.com](https://daneshyari.com)