



Predator learning differences affect the survival of chemically defended prey



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Prey animals that possess chemical defences often advertise their unprofitability to predators by a distinctive and conspicuous visual appearance known as aposematism. However, not all chemically defended species are conspicuous, and some are nearly cryptic. Differences in predator community composition and predator behaviour may explain varied levels of prey conspicuousness. We tested this hypothesis by measuring dietary wariness and learning behaviour of day-old chickens, *Gallus gallus domesticus*, from four strains of laying hens that have been selected for different levels of egg productivity. We used these strains as model predators to test whether predators that vary in the trade-offs associated with foraging behaviour cause differential survival of chemically defended prey with conspicuous signals. We found that strains differed in how they learned about chemically defended prey, which resulted in significant differences in prey survival. The selection pressures imposed by different types of predator could explain whether chemically defended prey evolve varied levels of conspicuousness. Predators' initial wariness of novel prey was not related to learning at the strain or individual level, but predator wariness increased after exposure to chemical defences. Our study provides support for the hypothesis that the evolution of prey defences depends on variation between ecological communities in predator learning behaviour and experience.

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Prey animals often advertise their chemical defences to predators by a distinctive and conspicuous visual appearance known as aposematic signalling (Wallace, 1889). Aposematism, which is typified by the red and black coloration of ladybirds (Majerus, Kearns, & Allington, 1989) and the black and yellow stripes of cinnabar moth caterpillars, *Tyria jacobaeae* (Aplin, Benn, & Rothschild, 1968), accelerates predator avoidance learning (Gittleman & Harvey, 1980; Roper & Wistow, 1986), and enhances predator memory of prey best avoided (Roper & Redston, 1987). Stronger, more visible signals facilitate faster avoidance learning than weaker signals, and can make the difference between predators learning or not learning to avoid aposematic prey (Alatalo & Mappes, 1996; Lindstrom, 1999; Mappes & Alatalo, 1997; Roper & Redston, 1987). However, not all defended prey advertise their defences with conspicuous signals (Arbuckle & Speed, 2015; Lindstedt, Huttunen, Kakko, & Mappes, 2011). Many chemically

defended species have variable colour patterns along their distribution range, for example polytypic poison frogs (Willink, García-Rodríguez, Bolanos, & Proehl, 2014), and polymorphic ladybirds and moths (Majerus et al., 1989; Nokelainen, Valkonen, Lindstedt, & Mappes, 2014). What causes some defended species to be distinctive and conspicuous and others inconspicuous?

This question has been explored theoretically, comparatively, and empirically (Endler & Mappes, 2004; Ratcliffe & Nydam, 2008; Valkonen et al., 2012). Theoretical models predict that differences in predator perception and/or learning behaviour can explain whether prey evolve aposematism rather than crypsis (Endler & Greenwood, 1988), aposematic polymorphisms (Mallet, 2001; Mallet & Joron, 1999; Mallet & Singer, 1987), or 'weak' aposematic signals (Endler & Mappes, 2004). Comparative analyses have revealed that tiger moths are more likely to deploy conspicuous visual warning signals when birds are their main predators, and ultrasonic clicks when bats are more prevalent (Ratcliffe & Nydam, 2008). Predators with different sensory capacities have also been implicated in how aposematic signal size varies in Japanese firebellied newts, *Cynops pyrrhogaster* (Mochida, 2011). These

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theoretical and comparative findings are supported by a number of empirical studies. For example, [Valkonen et al. \(2012\)](#), in an experiment with artificial snakes that were either warningly or not warningly coloured, found that in habitats dominated by specialist predators, artificial snakes with conspicuous warning signals were attacked more than inconspicuous snakes; in habitats dominated by generalist predators, the inconspicuous snakes were attacked more frequently than the conspicuous ones. Therefore, specialist predators may select for reduced conspicuousness, whereas generalist predators may select for conspicuous warning signals. Differences in the age/experience of predators can explain why aposematic signals are more prevalent in some seasons than others ([Mappes, Kokko, Ojala, & Lindström, 2014](#)). Furthermore, the predominant predator species in a habitat may have a greater influence on the maintenance of aposematic signal polymorphisms than less prevalent predator species ([Nokelainen et al., 2014](#)). These studies provide evidence that different predator behaviours can affect the fitness of aposematic signals and how they evolve.

[Guilford and Dawkins \(1991\)](#) proposed that differences in how a predator detects, discriminates, learns, and remembers a signal can represent a powerful selective force in signal design. Most research on predator behaviour and warning signals has focused on a single aspect of the predator's 'receiver psychology' ([Guilford & Dawkins, 1991](#)), such as detectability ([Siddiqi, Cronin, Loew, Vorobyev, & Summers, 2004](#)), discrimination ([Skelhorn & Rowe, 2006a](#)), or avoidance learning ([Ihalainen, Lindström, & Mappes, 2007](#)). However, the interaction between these different behaviours can affect selection on prey defences ([Skelhorn, Halpin, & Rowe, 2016](#)). A predator's ability to learn about prey types may be related to its initial reaction towards that prey ([Schuler & Roper, 1992](#)), and how predators learn can affect how they remember prey ([Ihalainen et al., 2007](#); [Roper & Redston, 1987](#)), and how they generalize their knowledge about those prey ([Gamberale-Stille & Tullberg, 1999](#)). In this study, we focused on two candidate predator behaviours that may differ across individuals and species and affect how warning signals evolve: differences in the initial responses towards novel and/or aposematic prey, and differences in the ability to learn to avoid aposematic prey ([Sherratt, 2002](#)).

Differences in the initial responses towards novel and/or aposematic prey can be characterized by a short-lived avoidance of novel/conspicuous prey (neophobia), or longer-term refusal to eat novel/conspicuous prey (dietary conservatism: [Exnerová et al., 2015](#); [Exnerová, Svádová, Fučíková, Drent, & Štys, 2010](#); [Marples & Kelly, 1999](#); [Marples, Roper, & Harper, 1998](#)). Neophobia and dietary conservatism are collectively referred to as dietary wariness. Predators that are wary of, and avoid attacking, novel and/or conspicuous prey may allow conspicuous signals to increase in abundance ([Marples & Mappes, 2011](#); [Richards et al., 2014](#); [Thomas, Marples, Cuthill, Takahashi, & Gibson, 2003](#)) to the extent that learned predator avoidance favours aposematism ([Lee, Marples, & Speed, 2010](#); [Mappes, Marples, & Endler, 2005](#); [Puurinen & Kaitala, 2006](#)). It has been argued that any selective benefit to conspicuous prey of being avoided by wary predators is transient at best ([Mallet & Singer, 1987](#)), because of variability in predator life span and wariness ([Lee et al., 2010](#)). However, varied levels of dietary wariness may promote the spatial mosaics of prey phenotypes that are seen in nature, especially if dietary wariness combines with differences in predator avoidance learning ([Lee et al., 2010](#); [Sherratt, 2002](#)). This prediction warrants empirical investigation.

Differences in predator avoidance learning are known to emerge because of differences in predator personality traits ([Exnerová et al., 2010](#)), developmental conditions ([Bloxham, Bateson, Bedford, Brilot, & Nettle, 2014](#)), nutritional state ([Barnett, Bateson, & Rowe, 2007](#)), and the complexity of the prey community in which the predator forages ([Ihalainen, Rowland, Speed,](#)

[Ruxton, & Mappes, 2012](#); for a comprehensive review of the factors that affect learning see [Skelhorn et al., 2016](#)). Variability of predator learning has been found to affect the fitness of aposematic prey and select for signal uniformity ([Halpin, Skelhorn, & Rowe, 2012](#); [Skelhorn & Rowe, 2007b](#)). Differences in predator learning could also explain the varied levels of warning signal conspicuousness, but this remains an open experimental question ([Endler & Mappes, 2004](#)).

Empirical studies that examine the links between predator wariness and learning are scarce ([Exnerová et al., 2010](#); [Sillen-Tullberg, 1985](#)). Neophobia/wariness may be unrelated to learning processes ([Braveman & Jarvis, 1978](#)). However, a warning signal to which predators are reluctant to respond by initiating an attack can theoretically induce faster avoidance learning and differential selection ([Guilford & Dawkins, 1991](#); [Rowe & Guilford, 1999](#); [Sherratt, 2002](#)). In a study with fast- versus slow-exploring predators, [Exnerová et al. \(2010\)](#) found that slow birds hesitated longer to attack novel aposematic prey, and subsequently took fewer trials to learn to avoid the same prey. However, the selection pressures imposed by these different types of predator did not result in differential mortality of aposematic prey. What remains unclear is whether differences in individual or species wariness combine with learning to produce differential selection pressures on prey, and if this can explain whether chemically defended prey evolve varied levels of conspicuousness.

To resolve this issue, we designed an experiment in which day-old domestic chicks, *Gallus gallus domesticus*, acted as model predators, as they have in much of the empirical research into wariness and the evolutionary dynamics of warning signal evolution ([Marples, Quinlan, Thomas, & Kelly, 2007](#); [Roper & Redston, 1987](#); [Roper & Wistow, 1986](#); [Rowe & Skelhorn, 2005](#)). There are intra- and interstrain differences in how chickens react to and learn about novel and/or aposematic prey ([Hauglund, Hagen, & Lampe, 2006](#); [Jones, 1986](#)). We propose that intra- and interstrain differences might be useful for the study of warning signal evolution, because they could be a simple way of simulating species and individual differences that are also observed in wild predators ([Adamová-Ježová, Hospodková, Fuchsová, Štys, & Exnerová, 2016](#); [Marples & Kelly, 1999](#); [Marples et al., 1998](#)). Intra- and interstrain differences can also provide information about feeding and learning in a domestic crop animal of major importance, and about the effects of selection on these behaviours ([Schütz, Forkman, & Jensen, 2001](#)).

We studied four laying strains of chickens that have been selectively bred for different levels of egg production and growth. Selection on these traits in modern poultry is linked to reduced fearful behaviours, compared to their wild-type ancestor, the red junglefowl ([Campler, Jöngren, & Jensen, 2009](#); [Schütz et al., 2001](#)). When populations of red junglefowl are selectively bred for a 'domesticated phenotype', traits similar to those of modern chickens emerge after only a few generations, e.g. larger body size, larger eggs and offspring ([Agnvall, Ali, Olby, & Jensen, 2014](#)), and increased boldness in novel object tests ([Agnvall, Katajamaa, Altimiras, & Jensen, 2015](#)). Based on this evidence for reduced fearfulness in high productivity lines, we predicted that (1) high productivity strains would exhibit lower dietary wariness (consume novel prey sooner) than lower production domestic strains.

High productivity strains also exhibit reduced contrafreeloading, i.e. prefer to choose easily accessible food over food that requires work ([Schütz & Jensen, 2001](#)). Reduced contrafreeloading results in individuals acquiring less information during foraging ([Lindqvist, Schütz, & Jensen, 2002](#)). From this we predicted that (2) high production strains would be less discriminating between foods and therefore acquire less information during learning (compared to strains that have lower productivity and growth), and therefore attack a higher proportion of chemically defended prey by the end of their learning phase. Based on the findings of

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