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Hairiness and warning colours as components of antipredator defence: additive or interactive benefits?

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To deter predator attack, aposematic prey species advertise their unprofitability with one or more conspicuous warning signals that, in turn, enhance the avoidance learning of predators. We studied the costs and benefits of multicomponent signalling in *Parasemia plantaginis* moths. The hairy moth larvae have an orange patch on their otherwise black bodies. The patch varies phenotypically and genetically in size. We studied whether the detection risk associated with patch size varied against two backgrounds (green or brown) with two different predators: naïve chicks, *Gallus gallus domesticus*, and experienced great tits, *Parus major*. We also evaluated the signal value of different defence traits within a multicomponent signal by testing which combination of two traits, hairiness and the presence or size of the orange patch, most affected the avoidance learning rate of predators. Larvae with a large orange patch were at greater risk of detection by birds against both backgrounds. This higher detection risk was traded-off with enhanced avoidance learning rate. The orange patch had a higher signal value for the predators than did hairiness, which only slightly increased the survival of totally black or small-patched larvae but did not affect the defence of larvae with a large orange patch. Multicomponent defences are therefore not necessarily additive and variation in the warning coloration of aposematic animals may be partly explained by variation in the relative benefits of different components of a warning signal to different predators.

Keywords: aposematism; multicomponent defence; *Parasemia plantaginis*; predation

Aposematism is an antipredator strategy where predators learn to associate the unprofitability of prey (e.g. chemical defences) with conspicuous and bright coloration, consequently avoiding similar prey in the future (Sillén-Tullberg 1985; Roper & Redston 1987; Alatalo & Mappes 1996; Gamberale & Tullberg 1996; Forsman & Merilaita 1999; Lindström et al. 1999; Ihalainen et al. 2007). Given the variation in predator susceptibility to aposematic prey defences, such as resistance to toxins (Calvert 1979; Fink & Brower 1981) or behavioural adaptation to overcome prey defence mechanisms (Yosef & Whitman 1992), many aposematic displays include many defence components simultaneously (Marples et al. 1994). Different defence components may be aimed at different predators with dissimilar search behaviour and perception (Pearson 1989) or against separate phases of predation (Endler 1991). Studies with real (Marples et al. 1994) and artificial (Rowe 2002) prey items have shown that the avoidance learning of a single predator becomes more effective if a prey species provides multiple defence cues (but see Vallin et al. 2005 for nonadditive benefits).

Empirical work on the function of multicomponent signals has concentrated on the interactions between warning coloration and odour (Rowe & Guilford 1999a; Lindström et al. 2001a; Kauppinen & Mappes 2003), sound (Rowe 2002; Hauglund et al. 2006) or grouping behaviour (Tullberg et al. 2000; Gamberale-Stille 2000). That many aposematic animals also use a physical trait, such as hair or spines, as a defence mechanism together with other antipredator repellents has been ignored until recently (Inbar & Lev-Yadun 2005; Speed & Ruxton 2005). Speed & Ruxton (2005) have shown mathematically that physical defences may act as visual cues to a prey's unprofitability and improve both the detectability of prey and the avoidance learning by predators. However, data that directly test the value of physical defences (e.g. spines or hairiness) as signals of unprofitability for visual

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predators and how they contribute to a prey individual's survival combined with other defence components are rare (but see Barnhisel 1991; Mikolajewski & Rolff 2004 for nonaposematic species).

We evaluated the signal value of two defence traits: hairiness and conspicuousness of the colour pattern. We asked whether physical defences such as spines or hair can (1) function as warning signals that enhance predators' avoidance learning rate, (2) function as secondary defence mechanisms that reinforce the effect of other defence components or (3) perform both of these functions simultaneously. Because conspicuousness incurs the cost of increased attention from predators (Riipi et al. 2001), we also tested possible differences in the conspicuousness of different prey morphs. We performed two separate experiments where we used wood tiger moth, *Parasemia plantaginis*, larvae as the prey species. *Parasemia plantaginis* is a useful model to test the interaction of colour and another physical trait in aposematic signalling because the larvae are hairy and have a moderately conspicuous orange patch, which varies in size phenotypically and genetically, on their otherwise black bodies (Ojala et al. 2007).

In the first experiment, we compared the relative detection risk of *P. plantaginis* larvae with small and large patches on two backgrounds: a dark brown background on which the larvae are rather cryptic and a green background on which the larvae are more visible. We used young, naïve domestic chicks, *Gallus gallus domesticus*, as inexperienced predators and wild-caught great tits, *Parus major*, as more experienced wild predators. We predicted that larvae with large orange patches would be more conspicuous, that is, more quickly detected, than larvae with small patches. We further predicted that detection time would be lower on the green background than on the brown background because of increased conspicuousness. Conspicuousness should be more costly when the predators are naïve domestic chicks than when predators are wild great tits that probably have already encountered warning-coloured unpalatable prey (see e.g. Lindström et al. 2001b).

The second experiment specifically examined the relative importance of the different defence components (hairiness and coloration) of the *P. plantaginis* larvae on avoidance learning rate by experienced predators, great tits. To test this, we first manipulated the hairiness (hairy or bald) and presence of the orange patch (patch or no patch) of the larvae (experiment 2a). We further (experiment 2b) investigated the effect of variation in warning coloration among prey on the avoidance learning rate of the predator. Hairiness was manipulated as in experiment 2a. We also manipulated the size of the orange patch (large or small).

We formulated three hypotheses that consider the relationship between hairiness and the size of the orange patch in experiments 2a and 2b (Fig. 1). Hypothesis 1 posits that both hairiness and patch size operate additively and improve prey defence, thus increasing the defence capacity of the prey (e.g. Rowe 1999). Therefore, if the orange colour patch is an important signal for predators, they should learn quicker to avoid prey with large patches than prey with smaller patches. Hairiness should make avoidance learning rate even more effective if it acts as a visual signal or deterrent (Inbar & Lev-Yadun 2005; Speed & Ruxton 2005). Both hypotheses 2 and 3 posit that hairiness and warning colour interact and, thus, hairiness could contribute to the defence capacity of prey with a large (hypothesis 2) or a small (hypothesis 3) colour signal (see Fig. 1b; e.g. Partan & Marler 2005).

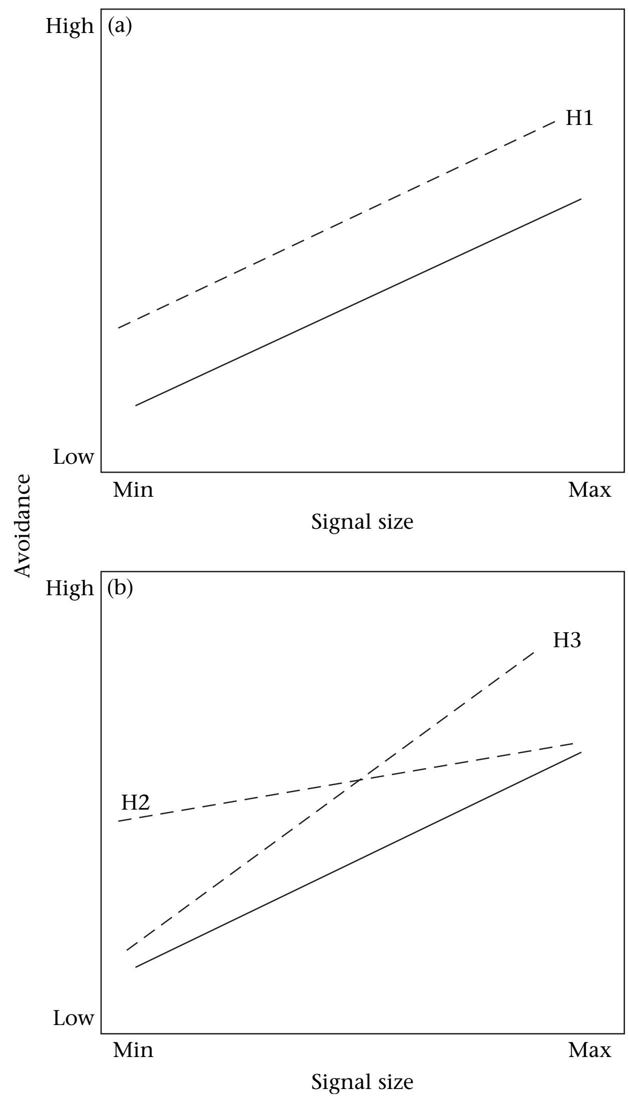

Figure 1. Hypothetical responses of predators towards prey with multicomponent warning displays. Three possible interactions between hairiness and signal size can be predicted: (a) hairiness and signal size additively increase defence capacity (H1) (Rowe 1999; Speed & Ruxton 2005), (b) hairiness contributes more to the defence capacity of prey with a weak signal (H2) or with a strong signal (H3). Dashed line shows the responses of predators towards the hairy prey and solid line shows the responses towards the hairless prey.

GENERAL METHODS

Parasemia plantaginis larvae and adults are warningly coloured and unpalatable for several different types of