

Change in protective coloration in the striated shieldbug *Graphosoma lineatum* (Heteroptera: Pentatomidae): predator avoidance and generalization among different life stages

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Abstract There are two major forms of protective coloration, camouflage and warning coloration, which often entail different colour pattern characteristics. Some species change strategy between or within life stages and one such example is the striated shieldbug, *Graphosoma lineatum*. The larvae and the pale brownish-and-black striated pre-diapause adults are more cryptic in the late summer environment than is the red-and black striation that the adults change to after diapause in spring. Here we investigate if the more cryptic pre-diapause adult and larval coloration may affect the aposematic function of the coloration as compared to the red adult form. In a series of trials we presented fifth instar larvae, pale or red adults to shieldbug-naïve domestic chicks, *Gallus gallus domesticus*, to investigate the birds' initial wariness, avoidance learning, and generalization between the three prey types. The naïve chicks found the red adults most aversive followed by pale adults, and they found the larvae the least aversive. The birds did not find the larvae unpalatable and did not learn to avoid them, while they learned to avoid the two adult forms and then to a similar degree. Birds generalized asymmetrically between life stages, positively from larvae to adults and negatively from adults to larvae. We conclude that the lower conspicuousness in the pale forms of *G. lineatum* may entail a reduced aposematic function, namely a reduced initial wariness in inexperienced birds. The maintenance of the colour polymorphism is discussed.

Keywords Aposematism · Camouflage · Crypsis · Domestic chick · Ontogenetic colour change · Warning coloration

Introduction

Insects often use one of two types of protective coloration. Some have a conspicuous warning coloration that deters predators by signalling their potential unprofitability as prey (Bates 1862; Darwin 1871; Poulton 1890; Cott 1940). Others use the strategy of camouflage,

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having a coloration that impedes discovery (Cott 1940; Edmunds 1974; Endler 1978; Ruxton et al. 2004). Although many species use the same type of defensive coloration throughout all life-stages, there are numerous examples of species that change strategy between or within life-stages (Wiklund and Sillén-Tullberg 1985; Kotaki 1998; Nylin et al. 2001; Musolin and Numata 2003; Grant 2007; Sandre et al. 2007; Tullberg et al. 2008). One of these species is the striated shieldbug *Graphosoma lineatum* L. (Heteroptera: Pentatomidae; Tullberg et al. 2008).

The adult of *G. lineatum* is mostly recognised for its conspicuously red (epidermis) and black (melanised cuticula) striated coloration (Fig. 1). However, in south-central Sweden, the new adults of *G. lineatum*, that eclose in late summer, lack most or all of the red pigmentation in their coloration. Instead of the red colour, the epidermis is pale, light brownish (Tullberg et al. 2008; Fig. 1), which match the background of dried umbels and stems of the host plants (various apiaceaeous species, e.g. *Anthriscus sylvestris*, *Aegopodium podagraria*, *Angelica sylvestris* etc.) on which the bugs are found. This is supported by the reflectance spectra of the two adult colour forms as well as dry umbels of *A. sylvestris* in Tullberg et al. (2008). The pale adults go into diapause in the ground during winter and appear again in the lush green early summer environment, now characteristically coloured red and black. The larvae have an inconspicuous coloration of different shades of brown and black, suggesting a cryptic, non-signalling, function (Fig. 1). Unfortunately, we have not yet managed to obtain comparable measurements of larval coloration because of the smaller colour patches and the softer larval cuticula.

Aposematism is a strategy where toxic, or otherwise unprofitable prey, use a conspicuous warning coloration as an avoidance-inducing signal of defence to predators (Poulton 1890; Matthews 1977). Conspicuous colour patterns that contrast with the background have been shown to reduce attacks from inexperienced predators (Roper and Cook 1989; Lindström et al. 2001) and accelerate learning (Gittleman et al. 1980; Roper and Cook 1989; Roper and Redston 1987; Riipi et al. 2001). Contrast with the background also enhances recognition and memorability (Roper and Redston 1987; Gamberale-Stille 2001). Thus, there are several possible signal related benefits in having a contrasting conspicuous colour pattern. On the other hand, a conspicuous colour pattern also entails the obvious risk of discovery by uneducated and indifferent predators.

Several experimental studies show that the red form of *G. lineatum* is well defended against small insectivorous birds and is avoided after a few attacks (Schlee 1986; Vesely



Fig. 1 The prey types used in the experiment: from left to right, a fifth instar larva ('L5'), a newly eclosed late summer adult ('Pale') and a post hibernation early summer adult ('Red') of the striated shieldbug *Graphosoma lineatum*

et al. 2006; Exnerová et al. 2008), suggesting an aposematic function for the red-and-black coloration. The pale autumn form, found in Sweden, also possesses functional stink glands and a bioassay suggests that it too is unpalatable to birds (Tullberg et al. 2008). A recent study, using human subjects searching for prey on a computer screen, shows that the pale form of *G. lineatum* is harder to discover than the red form in the late summer habitat (Tullberg et al. 2008). A similar study also reveals that the larvae are more cryptic than the red form (unpublished results). Additionally, great tits (*Parus major*) initially take more time to find the pale than the red adult form in a semi-natural environment of dry grass and host-plants (Johansen et al. MS). Thus, the larvae and the pale adult form seem to be more cryptic than the red adult form in the late summer environment in which they naturally occur. Because conspicuousness is an important factor for producing efficient avoidance learning, the benefits gained from a reduced risk of discovery (i.e. reduced conspicuousness) in the pale forms may entail a cost of impaired aposematic signalling function.

The aim of this study is to investigate possible costs and benefits of the different forms of *G. lineatum* with respect to the aposematic defence. To be able to investigate birds' initial unlearned aversion as well as avoidance learning and generalization between the forms, we use naïve domestic chicks (*Gallus gallus domesticus*) as predators.

Materials and methods

We used male domestic chicks (*Gallus gallus domesticus*) as predators, under permit from Stockholms Djurförsöksetiska Nämnd, DNr: N191/07. We obtained a total of 84 chicks, in two consecutive batches, from a commercial hatchery. On arrival, the birds were less than 24-h old and had not yet been fed. The birds were housed in two cages measuring $55 \times 100 \times 20$ (width \times length \times height), with steel-net floor, wooden sides, one half of the roof made of chicken wire and the other half made of wood. The floor was covered with wood chips and the part with the wooden roof was heated with a 60W carbon filament lamp. The birds always had free access to chick Starter crumbs (Pullfor) and water ad lib, when not taking part in testing. Thus the birds were not food-deprived prior to experiments. We occasionally fed the birds with mealworms (*Tenebrio molitor*) in the cages to familiarise them with live prey. Umbels of Cow-Parsley, *A. sylvestris*, were placed in the cages to familiarise them to the objects used later in the experimental setup.

As experimental prey in the experiment we used fifth instar larvae ('L5') and adults of both the early and late summer colour forms ('Red' and 'Pale', respectively) of *G. lineatum*. All prey were taken from laboratory cultures of *G. lineatum*, originally collected from the Stockholm area, Sweden. All bugs were reared at light:dark regime of 12:12 h, on seeds of *A. sylvestris* and *A. podagraria*, fresh cultivated parsley (*Petroselinum crispum*) and pieces of freshly cut carrot (*Daucus carota sativus*). All bugs were initially reared together at 26°C. The fifth instar larvae ('L5') and newly eclosed 'Pale' adults were moved into to 17°C. In this way they were kept as larvae for longer, and the 'Pale' adults did not change colour and become reproductive. The 'Red' adults were individuals from the same culture that had already attained a red coloration.

Experiments took place in an arena shaped as a corridor measuring $20 \times 120 \times 30$ cm (width \times length \times height), with the floor covered with wood chips. The experimental arena was in the same room as the housing cages, and the room was lit by daylight from the windows, by daylight-strip lights (OSRAM BIOLUX L36W/72, now very low in UV) and four fluorescent strip-lights (OSRAM L36W/73, emits light between 350 and 420 nm), between 0800–2000 hours. All prey were placed upon a dry umbel of cow-parsley laying

on a transparent plastic plate (10 cm in diameter) situated in the middle of the length of the arena (60 cm from the ends). At the start of the pre-training sessions and during experiments the chicks were placed at one end of the arena and thus had to approach the prey to attack it.

Prior to the experiments, the chicks were successively trained to forage for live prey alone in the arena. For this we used mealworms presented in the same way as the *G. lineatum* later in the experiments. Chicks were first allowed into the arena in small groups, then in pairs, and eventually they were foraging singly in the arena. At the start of the experiment, all chicks readily approached and ate mealworms alone in the set-up. The experiments started on the chicks' sixth day. At the start of the experiments, the chicks from each batch were divided into three experimental groups that received one of either prey type ('L5', 'Pale' or 'Red') as the first prey presentation (Prey 1). All birds were also presented with a second prey (Prey 2), so each group above was again divided into three subgroups, receiving one of either prey type ('L5', 'Pale' or 'Red'; Table 1).

The prey presentations followed a certain scheme: Each chick was presented prey twice a day, once in the morning and once in the afternoon. All presentations had the duration of 60 s, independently of whether or not an attack occurred. All experimental prey presentations were also followed by a mealworm presentation, to control that the chicks were hungry for live prey. Each chick was first presented with Prey 1 for two to six possible presentations. After two consecutive non-attacks, or, in total, three attacks on Prey 1 the chicks were presented with Prey 2. These criteria were chosen because we had a limited number of bugs available for the experiment, and the mortality risk was potentially unequal between prey types; the larvae are relatively edible and soft bodied compared to the adults. The second prey type was only presented once. Data was collected about whether or not a prey was attacked, eaten and killed, and was analysed using two-tailed Contingency tables (Fisher exact probability test for 2×2 tables, and the Freeman-Halton extension of the Fisher exact probability test for 2×3 tables, Freeman and Halton 1951). We also collected information about attack latencies, but it was shown that birds decided very early in a trial whether to attack or not, so the times did not provide any extra information and was not included in the analysis.

Results

The naïve birds differed in how they reacted to the three prey types (Fig. 2). There was a difference in the number of birds attacking their first prey type, Prey 1, (Table 1, Fisher Exact Test, $P < 0.0001$). The birds found the 'L5' more attractive than both other prey

Table 1 The experimental set-up showing the number of attacking birds and sample sizes in the experiment

Prey 1 (attacking birds/N)	Prey 2 (Attacking birds/N)					
	All birds			Only birds that attacked Prey 1		
	Larvae	Pale adults	Red adults	Larvae	Pale adults	Red adults
Larvae (29/30)	10/10	9/10	9/10	10/10	8/9	9/10
Pale adults (21/27)	4/9	1/9	3/9	4/6	1/6	3/9
Red adults (13/27)	5/9	2/9	5/9	2/3	1/6	3/4

types ('L5' vs. 'Pale': the treatment with the next highest attack probability: Fisher Exact Test, P -value = 0.0446). Noticeably, the birds also found the 'Red' adults initially more deterrent than the 'Pale' adults (Fisher Exact Test, $P = 0.047$; Fig. 2). Thus, the naïve chicks found the 'L5' larvae the most attractive followed by the 'Pale' adults, and they found the 'Red' adults the least attractive.

Also, there was a difference between treatment groups in how many of the attacking birds that stopped attacking during the presentations of Prey 1, following the criteria of two consecutive presentations without attacks ('L5': 1/29, 'Pale': 14/21 and 'Red': 7/13, Fisher Exact Test, $P < 0.0001$). There was no significant difference between 'Pale' and 'Red' treatment groups (Fisher Exact Test, $P = 0.491$), but fewer birds presented with 'L5' stopped attacking Prey 1 than the other two types ('L5' vs. pooled adults, Fisher Exact Test, $P < 0.0001$). Thus, more chicks avoided the adults after attack than the 'L5' larvae, but there was no difference between groups presented with the two adult colour forms.

To investigate the birds' generalization of their experience of Prey 1 to Prey 2, we only looked at the behaviour of birds that had attacked their first prey type, but the results are generally the same also if we include birds that had seen but not attacked Prey 1 (Table 1). In total, there was no difference between birds with prior experience of the adult forms in their attack probability of Prey 2 (8/21 'Pale' and 6/13 'Red', Fisher Exact Test, $P = 0.728$). However, more birds with 'L5' experience attacked the second prey type than did birds with experience of the adult forms (27/29 'L5' and 14/34 adults (pooled), Fisher Exact Test, $P < 0.0001$). Moreover, a prior experience of one of the two adults reduced attacks on 'L5' compared to when naïve (Fisher Exact Test, $P = 0.032$), and conversely, a prior 'L5' experience increased attacks on the adult forms (Fisher Exact Test, $P = 0.041$) compared to when naïve (Fig. 3). Thus, predators' prior experience of the larvae increases attack risk for the adults, whereas a prior experience of one of the adult forms reduces attack risk for the fifth instar larvae.

There also seems to be a difference in palatability between the prey types. Of all chicks that attacked during the Prey 1 presentations, none of them ate an adult whereas 21 out of the 29 chicks attacking 'L5' ate one or more prey (Fisher Exact Test, $P < 0.0001$).

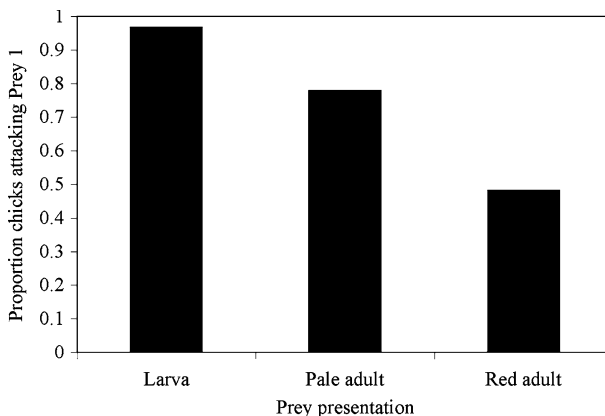


Fig. 2 The initial aversive effect of prey types illustrated as the proportion of attacking naïve birds in three experimental groups when presented with single fifth instar larvae, 'Pale', or 'Red' adults during their Prey 1 presentations

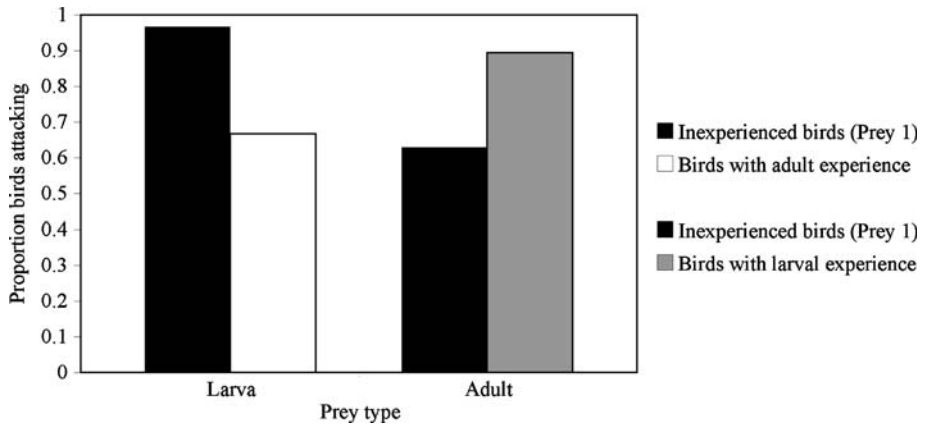


Fig. 3 Predator generalization between prey types compared to the behaviour of inexperienced birds, illustrated as the proportion of birds attacking when presented either with the fifth instar larvae or one of the two adult forms. *Black bars* represent inexperienced birds presented with Prey 1. *White and grey bars* represent birds with prior adult or larval experience, respectively. Thus, all attack behaviour of birds presented with the two adult forms is pooled into adult categories. Only birds that attacked their prey during the Prey 1 presentation are included in the generalization data

Discussion

In this study we show that the seemingly cryptic fifth instar larvae of *G. lineatum* is less defended against birds than the adults are. Most birds presented with a larva as their first prey type attacked the prey, suggesting that they were not deterred by its appearance. Even though the fifth instar larvae possess stink glands that may emit noxious compounds (Stransky et al. 1998; pers. obs.), many chicks found them quite palatable. We cannot distinguish from this experiment why the birds' ate the larvae to a greater extent than the adults. The difference could for instance both be due to the quality of the chemical defences, and the fact that the larvae have a considerably softer cuticula than the adults. In any case, this result may explain the non-conspicuous appearance of *G. lineatum* larvae in that they may have a too weak secondary defence against birds to sustain an aposematic strategy. The two adult forms, however, seemed to have a more effective secondary defence because most birds stopped attacking the prey after a few encounters, and almost none of the adults were killed or eaten after attacks. These results support previous studies on the effective defence of *G. lineatum* adults against bird predation (Schlee 1986; Exnerová et al. 2003, 2008; Vesely et al. 2006).

Importantly, there was a clear difference in how aversive the chicks found the appearance of the Pale and the Red adults. More birds refused to attack the Red form of the bug when presented as their first prey type. This result is similar to that of Sillén-Tullberg (1985), where great tits (*Parus major*) showed a greater wariness to attack the normal aposematic red-and-black larva of the heteropteran bug *Lygaeus equestris*, as compared to a mutant form that lacked the red pigments. Similarly, in experiments with several wild bird species and different colour mutants of *Pyrhocoris apterus*, Exnerová et al. (2006) showed the importance of colour for bird avoidance of another normally red-and-black heteropteran species. In our experiment, the difference in initial avoidance between forms, especially the two adult forms, could be due to both possible hue specific intimidating effects, as have been

shown previously for red insect prey, and/or due to a greater contrast against the background in the red form (reviewed in Ruxton et al. 2004). Thus, taken together, the lower wariness towards the ‘Pale’ form of *G. lineatum* in our experiment, suggests that the reduced conspicuousness of the coloration (as shown in Tullberg et al. 2008; Johansen et al. MS) results in a weakened aposematic effect, i.e. a reduced avoidance response.

Both background contrast and hue specific effects could also potentially affect avoidance learning (e.g. Roper and Cook 1989; Ruxton et al. 2004; but see Ham et al. 2006). Yet, we did not find any difference between the two adult colour forms in how they affected the speed of avoidance learning, here measured as the number of birds that stopped attacking the two types during the first prey presentation series. However, as we do not know whether or not the two forms also differ in unpalatability and, as the degree of unpalatability is another important factor affecting the speed of avoidance learning, it is not possible to tease out the effect of coloration alone on learning in this experiment. Also, it is likely that the discrimination task in this study (between mealworms and one novel shieldbug) was too simple to be able to discern any possible differences in the effects on learning. Then again, it has been convincingly argued that conspicuousness may not be necessary to produce a functional warning signal as long as the unpalatable prey is distinct enough from palatable prey to allow an easy discrimination (Sherratt and Beatty 2003; Merilaita and Ruxton 2007). However, when a signal is not costly to cheaters the system cannot be an evolutionary stable strategy (e.g. Maynard Smith and Harper 2003 and references therein). Conspicuousness is the most probable candidate to provide such an unequal cost to models and cheaters, as it would increase the attack rate of uneducated or indifferent predators; a selective force could then act against cheaters that lack a secondary defence (see also Gamberale-Stille and Guilford 2004; Ruxton and Speed 2006). Thus, aposematic systems without the cost of conspicuousness may be quite rare, if at all possible.

The results from the generalization test suggest that the birds generalized quite broadly between the prey. An experience of the larvae resulted in an increased risk of attack on the adults. Conversely, the larvae gained protection from the birds’ generalization from the prior negative experience of the adults. The results suggest that the great initial wariness in naïve chicks towards the red-and black form, and to a lesser extent the pale light brown-and-black form, is quite easily affected by the previous experience of the birds (here the palatable larvae, Fig. 2). These results imply an asymmetric relationship between larvae and adults in how they benefit from co-occurring with respect to predation risk (see Svádová et al. 2009 for further discussion of asymmetric predator generalization among aposematic bugs). In the field, it is mostly the ‘Pale’ adults and the fifth instar larvae that overlap in both space and time. Thus, in effect, the larvae may gain some protection from co-occurring with the ‘Pale’ adults whereas the ‘Pale’ adults may obtain a cost from the positive generalization from the larvae. However, the net effect on predation risk from co-occurring between the larvae and pale adults is probably more complex than this. For instance, it has been shown that birds may bias their generalization in favour of patterns with the same hue but higher contrast (Osorio et al. 1999). When superficially comparing the internal contrasts of larvae and pale adults (Fig. 1), it is possible that the adult colour pattern consists of similar hues as the larvae but with more contrasts, although a more objective analysis of colour pattern differences is needed to draw any firm conclusions. Therefore, as the larvae also have a chemical defence and some predators probably learn to avoid them, the generalization from these predators may instead benefit the adults.

As mentioned, the newly eclosed, pale brown-and-black striated *G. lineatum* adults appear in late summer when they, like the larvae, sit quite motionless on the dry stems and umbels, mostly feeding on seeds of their apiaceaeous host plants. These pale adults later go

into diapause, hiding under leafy litter in the ground (Stehlik 1984; C.-C. Coulianos, pers. com.). Our study suggests that the reduced conspicuousness in the dry late summer environment of the pale form, as compared to the red-and-black early summer form (as shown by Tullberg et al. 2008; Johansen et al. MS), entails a cost in terms of a less efficient aposematic signal. It seems as if the most sedentary forms, the larvae and the pale late summer adults, possess a more cryptic primary defence strategy, whereas the more mobile early summer adults clearly have adopted an aposematic strategy (Johansen et al. unpublished data). This situation is in line with the ideas that emphasize that a cryptic strategy involves constraints, or opportunity costs, that may facilitate the evolution of aposematism (Edmunds 1974; Guilford 1988; Merilaita and Tullberg 2005; Speed and Ruxton 2005). However, in the case of the Swedish *G. lineatum*, it is possible that the costs related to crypsis are quite small in the pale late summer adults because they do not need to move about so much. Later, after diapause, the conspicuous red-and-black coloration coincides with reproduction that demands increased exposure and mobility. Thus, we suggest that this colour polymorphism between the different life-stages may be maintained by a greater benefit to crypsis in larvae and pale adults, as these co-exist with a low activity phase in the life-cycle, whereas in spring the situation switches and an aposematic strategy is more beneficial as the individual needs to move around to reproduce.

Another important factor that may maintain the polymorphism between life stages in this system is discussed in Tullberg et al. (2008). As the different colour forms occur at different times during the season, the age composition of the predator community differs. It is possible that the red, conspicuous form that occurs in spring is faced with mostly adult bird predators that are potentially more educated with respect to aposematic prey. When the pale adults emerge in the late summer, however, the predator community also includes yearlings that are likely to be less experienced. This means that the cost of being conspicuous may be much greater in autumn because of the higher risk of being attacked by inexperienced predators. This idea is supported by the model by Endler and Mappes (2004), which showed that the composition of predator types (e.g. those that learn about unpalatability and those that are indifferent to the defence) might affect which primary defence strategy, conspicuous signalling or crypsis, is favoured in unprofitable prey.

The distribution of *G. lineatum* ranges from Europe and North Africa to western Asia (Wagner 1956). Sweden is part of the northernmost distribution and the species seems to be expanding northwards. The occurrence of the pale form of *G. lineatum* has also been reported from central and southern Europe (Wagner 1956; Stichel 1960). If an adaptation related to conspicuousness is a general explanation for the colour difference between the pre- and post diapause forms found in Sweden, we predict that the non-red form of adult *G. lineatum* should occur in association to a non-reproductive more sedentary stage of the life cycle in other parts of its distribution.

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