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Life-history constraints and warning signal expression in an arctiid moth

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Summary

1. Traditionally, large pattern elements in conspicuous warning signals are assumed to be selected by predation because increasing signal strength enhances education and avoidance of predators. However, variation in the colour pattern of a warningly coloured species often exists even within a location, and many warning signals have relatively small pattern elements. This suggests that there must be opposing selection pressures that can constrain warning signal expression, resulting in variation in warning signals as well as suboptimal signals for predator education.

2. We quantified the variation in the warning signal of *Parasemia plantaginis*-moth larvae. With a full-sib rearing experiment, we tested whether this variation has a genetic as well as an environmental component, by measuring the warning signal size of the developing larvae that were reared on either *Rumex* or an artificial diet. We also measured whether signal development was correlated to other life-history variables.

3. We show that the relative size of the warning signal varies among families but increases with larval age. The signal development also has an environmental component, since signal size develops more slowly and remains smaller in larvae feeding on the artificial diet than in those feeding on *Rumex*. Also, larvae with a short development time produced large warning signals. We also found that the larvae with a large orange signal were more likely to survive to adulthood.

4. Our results suggest that diet and life-history correlates can constrain development of the warning signal. Our study underlines the importance of considering life-histories of animals, not only predation, when studying the evolution of warning signals. Constraints of multiple selection pressures should be incorporated into the theory of the evolution of aposematism.

Key-words: life-history, *Parasemia plantaginis*, aposematism, predator–prey interactions, warning signals

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Introduction

Animals that are unpalatable to potential predators often have a warning signal, which indicates that attack against the individual would be futile, costly or even dangerous (Poulton 1890; Cott 1940; Edmunds 1974). This defence strategy is termed aposematism. It works because predators learn to avoid attacking signalling unprofitable prey and thus reduces the risk of the aposematic animal being harmed by a predator (Gittleman & Harvey 1980; Guilford 1990). Since warning colours are aimed at predators, most of the aposematism research has concentrated on the study of the signal efficacy, particularly on how the properties of aposematic signals affect predator behaviour (see Ruxton, Sherratt & Speed 2004). It has been argued (Wallace 1867; Cott 1940; Sherratt & Beatty 2003) that aposematic signals should evolve towards conspicuous and large pattern elements, since these traits are easier for predators to learn, recognize and avoid (Sillén-Tulberg 1985; Roper & Redston 1987; Roper 1994; Lindström *et al.* 1999, 2001; Hagman & Forsman 2003; Sherratt & Beatty 2003), although both predator type (Endler & Mappes 2004; Mappes, Marples & Endler 2005; Exnerova *et al.* 2007) and detection distance (Tullberg, Merilaita & Wiklund 2005) can affect this prediction.

However, contrary to these theoretical expectations and benefits shown of large pattern elements by induced predator avoidance learning (Sillén-Tulberg 1985; Roper & Redston 1987; Roper 1994; Alatalo & Mappes 1996; Forsman & Merilaita 1999; Lindström

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et al. 1999, 2001), there can be considerable variation in the aposematic signals within species even within localities (Brown & Benson 1974; Brakefield 1985; Owen *et al.* 1994; Majerus 1998; Gordon & Smith 1999; Sword 1999). This variation indicates that other factors besides predation affect the colouration of aposematic animals. For instance, several environmental factors are known to affect animal colouration (e.g. Slagsvold & Lifjeld 1985; Fields & McNeill 1988; Heal 1989; Hazel 2002), and thus they can be assumed to produce variation in the warning signal of an aposematic organism.

In addition to warning function, colours and colour patterns can serve a diversity of other functions in insects, such as thermoregulation, protection against UV radiation, sexual signalling, crypsis or disruptive colouration. Due to these different functions, there may also be several possibly opposing selection pressures on colour expression. Thus, although warning signals with large pattern elements give best protection against predators (Gamberale & Tullberg 1996; Forsman & Merilaita 1999; Lindström *et al.* 1999; Jansson & Enquist 2005), production and maintenance costs as well as different environmental conditions may constrain warning signal expression. For example, diet has been found to affect the brightness and hue of aposematic ladybird colouration (Grill 1999). The effect of diet on colouration can therefore be particularly pronounced in polyphagous herbivore species, since their host plants can differ greatly in their chemical properties. If a colour or a colour pattern is used for several functions, it is likely that it represents a local trade-off among the various functions (Endler & Mappes 2004), which could also explain the paradoxical variation in the warning signals.

Parasemia plantaginis L. (Arctiidae) is a warningly coloured species both as a larva and an adult. Larvae feed on numerous herbaceous and arborescent plant species (Marttila *et al.* 1996), and their life-history traits and immunocompetence are affected by their larval diet (Ojala *et al.* 2005). The hairy larvae have a patch of orange hair on their dorsal side. In combination with an otherwise black body, this orange patch is a warning signal to potential predators. The larger the orange signal is, the faster the predators learn to avoid a larva (Lindstedt *et al.* unpublished data). However, the detection risk is greater when the orange path is larger, and the cost–benefit ratio of a large signal thus depends e.g. on the frequency of educated vs. naive predators in the environment. Also, the hairiness of the larva can affect predator learning, but only when the orange signal is small or when it is absent (Lindstedt *et al.* unpublished data).

In this study, we investigate genetic and environmental factors influencing warning signal expression. In particular, we were interested in the factors constraining the warning signal expression. We ask: (i) How much variation is there in the size of the warning signal of *P. plantaginis* larvae? (ii) Is the size of the signal genetically determined? (iii) Does the environment, especially diet, affect signal size? (iv) Is the level of phenotypic and genetic variations in the signal size correlated with life-history traits, e.g. growth? Combining the life-history theory perspective and aposematism theory will help us understand why aposematic organisms sometimes have apparently not maximized the effectiveness of their defence (see also Longson & Joss 2006), even though that is what we would predict if we ignore the costs and benefits of a defence strategy other than the ones directly derived from predation.

Materials and methods

LIFE-HISTORY OF *PARASEMIA PLANTAGINIS*

In our study area at Åland, adult moths emerge between mid-June and mid-July, depending on the weather conditions. Adults live for only a few days after emergence, and females lay *c.* 200 eggs in clusters. After hatching, polyphagous larvae (five to seven larval stages) actively search for suitable host plants and start feeding. *Parasemia plantaginis* typically overwinter as a fourth instar larvae. However, in warm summers and in laboratory conditions, larvae continue feeding and second generation emerges. In Finland, second generation may be possible only in Åland and in the southernmost parts of Finland. In Central Europe, a second generation seems to occur regularly (Marttila *et al.* 1996, own observation).

REARING

Thirteen adult *P. plantaginis* females were caught before 10 July 2003 in Jomala, Åland Islands in southwestern Finland. All the females were from a single population, had mated in the field and laid eggs in plastic containers after capture. We reared *P. plantaginis* larvae ($n = 117$) in Jyväskylä in southern Finland on two diets: their natural host plant *Rumex longifolius* and a semolina-based artificial diet (modified from Poitout & Bues (1974) by leaving out ascorbic acid and formaldehyde and adding 0·5% Vanderzant vitamin mixture for insects). The purpose of having these two diets was to produce two different-quality environments. *Rumex* is beneficial for larval growth, survival, immunocompetence and fecundity, whereas the artificial diet is sufficient for the survival of the moths but results in slow growth, low immunocompetence and low fecundity (Ojala *et al.* 2005). Therefore, we could expect that if there is an environmental component to the production and maintenance of an aposematic signal, there would be a difference in the signal size of the larvae reared on different diets.

Larvae were randomly distributed to individual Petri dishes on their hatching day, with a maximum of five larvae per family allocated to each diet. Food was placed *ad libitum* in the Petri dish and replaced with fresh food every day. Larvae were reared in a greenhouse where the lighting and temperature followed roughly the outside conditions. Eighty-seven larvae pupated. They were weighed on the day of pupation and transferred to individual plastic containers. However, the pupation event of five individuals was missed, and those individuals were not weighed and the growth rate could not be calculated, and thus, the final sample size for the analyses in which growth rate was included was 82. Adults emerged 5–11 days after pupation, and they were sexed at this point.

WARNING SIGNAL SIZE ASSESSMENT

The moulting of the larvae was checked every day. Larvae gained their dorsal orange patch in their fourth instar. After gaining an orange patch, the larvae were photographed in each instar, 1 day after a moult was recorded. The larvae were anaesthetized with CO_2, stretched to full length and photographed with a Canon D 60 digital camera in standard lighting conditions. The number of larval instars per individual varied, and we therefore had two to four digital images of each larva. Both the total length of the larva and the length of the orange patch were measured from each digital photograph with ImagePro Plus 4·0 (Media Cybernetics, Bethesda, MD, USA). In most larvae, we measured only the length of the patch, since the length of the orange patch correlates positively with the width of the patch ($n = 20$, $r = 0{\cdot}796$, $P < 0{\cdot}001$) and since the orange colour spreads to the sides of the larvae when the signal is large, thus making the measurement of the width of the patch unreliable from the photographs that were taken from above only.

STATISTICAL ANALYSIS

To study the effect of diet and family on the size of the warning signal in the fourth and the last instars before pupation (depending on an individual, fifth to seventh instar), we used an ANCOVA with the log length of the patch as the dependent factor and the log length of the larva as a covariate. In all other analyses, we used the relative size of the orange patch (log length of the orange patch minus log length of the larva). Relative size of the warning signal did not differ between sexes either in the fourth (one-way ANOVA $F_{1,82} = 0{\cdot}010$, $P = 0{\cdot}922$) or in the last instar (one-way ANOVA $F_{1,82} = 0{\cdot}001$, $P = 0{\cdot}972$), and thus, we did not include sex as a factor in the analyses, but it was included in analysis of the other life-history traits. In the cases when the data did not meet the assumptions of ANOVA, we used the ranked values for the analyses. To analyze the relationship between likelihood of death before adulthood and signal size, we used binary logistic regression, with the size of the individual included in the model. For visual clarity, in Figs 1 and 2, we used length of the orange patch/length of the larva as a measure of the relative size of the signal. We analyzed the data using SPSS 12·0·1, and all P values are two tailed.

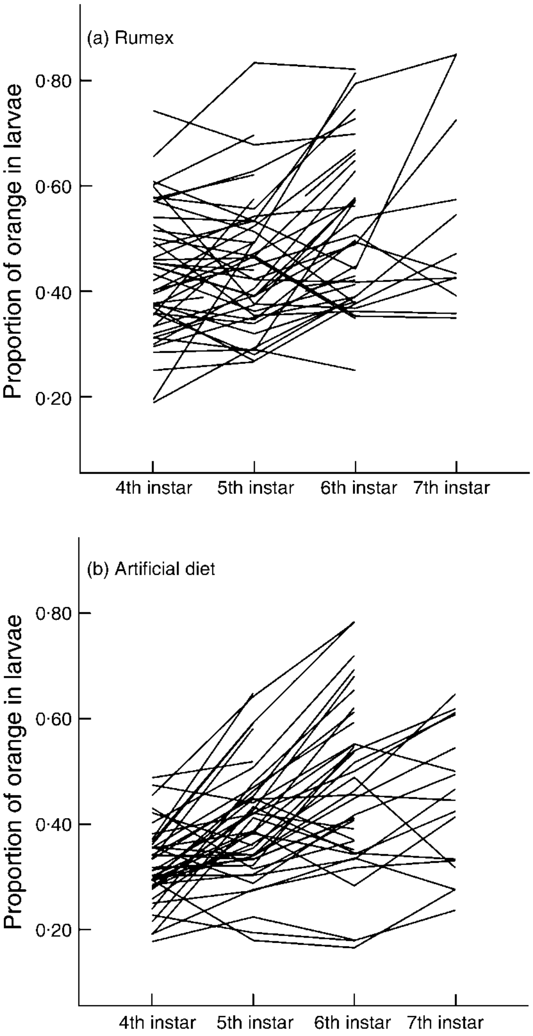

Fig. 1. Variation in the warning signal size (orange patch on the black) in different instars between diets, (a) *Rumex* and (b) artificial diet. Each line represents the development of the warning signal size of an individual larva. Since larva had variation in the instar numbers, the end point of each line represents the signal size at the 'last larval instar' before pupation.

Results

We found high levels of variation in the size of the warning signal of *P. plantaginis*: there was variability in the size of the orange patch both during the growth of an individual moth and among individuals in an instar. Larval colouration varied from almost black individuals to mostly orange (mean proportion of orange in the fourth instar larvae on *Rumex* = 0·416, SD = 0·119; artificial diet mean = 0·321, SD = 0·071; mean proportion of orange in the last instar on *Rumex* = 0·536, SD = 0·156; artificial diet mean = 0·488, SD = 0·149; Fig. 1). The variation of the relative size of the warning signal in both the fourth and the last instars on both diets had a normal distribution (one-sample K–S test all Z values < 0·6, all P values > 0·5), indicating that variation in the size of the warning signal was continuous and not based on distinct morphs.

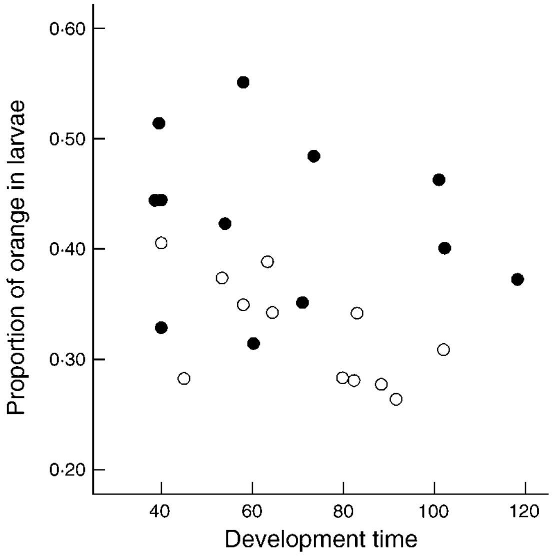

Fig. 2. Correlation between larval development time and the relative size of the warning signal (length of the orange patch/length of the larva in the fourth instar). Each dot represents a family mean of each trait on either *Rumex* (solid circles) or artificial diet (open circles).

Table 1. ANCOVA, with the log size of the larvae (length) as a covariate, on the effect of diet (fixed) and family (random) on the log size of the warning signal in the fourth instar and the last instar before pupation

Source of variation	df	Mean square	*F*	*P*
Fourth instar				
Diet	1	0·106	28·932	<0·001
Family	12	0·030	3·040	0·030
Diet × family	12	0·024	0·982	0·472
Size	89	0·407	39·541	<0·001
Error	89	0·010		
Last instar (fifth, sixth or seventh)				
Diet	1	0·043	10·746	0·005
Family	12	0·045	4·407	0·007
Diet × family	10	0·017	0·808	0·641
Size	64	1·213	131·074	<0·001
Error	64	305·200		

The relative signal size was significantly larger in the last instar than in the fourth instar (Wilcoxon signed ranks test $Z = -6·776$, $P < 0·001$; on *Rumex* $Z = -3·787$, $P < 0·001$; on artificial diet $Z = -5·643$, $P < 0·001$; Fig. 1). There was a significant positive within-individual correlation between the relative size of the patch in the fourth and the last larval instars ($r_s = 0·406$, $n = 91$, $P < 0·001$ (on *Rumex* $r_s = 0·367$, $n = 45$, $P = 0·013$; on artificial diet $r_s = 0·478$, $n = 46$, $P = 0·001$). This indicates that the larvae which had a small signal in the fourth instar also had a relatively small signal in the last instar.

Both diet and family significantly affected the size of the warning signal (Table 1). On the *Rumex* diet, signal size was significantly larger than on the artificial diet (Fig. 1). The family × diet interaction was non-significant, which means that although there were significant differences among families in signal sizes, all families responded similarly for the diet manipulation (Table 1). Thus, we managed to create good (*Rumex*) and poor (artificial diet) environments with respect to the signal development.

We did not find that feeding on *Rumex* was clearly better than on an artificial diet; however, there was a significant diet × family interaction in both the pupal mass (ANOVA for square root-transformed data $F_{10,57} = 2·010$, $P = 0·049$) and the development time (ANOVA for ranked data $F_{10,62} = 2·418$, $P = 0·017$). Thus, the ability to grow by feeding on different diets varied among families. The means in development time and relative signal sizes for families in the fourth and last instars were strongly negatively correlated for larvae feeding on an artificial diet ($r_s = -0·650$, $n = 12$, $P = 0·022$; $r_s = -0·636$, $n = 11$, $P = 0·035$, respectively). For larvae feeding on *Rumex*, the correlation was significant in the last instar larvae but not in the fourth instar larvae ($r_s = -0·701$, $n = 12$, $P < 0·011$; $r_s = -0·189$, $n = 12$, $P = 0·556$, respectively; Fig. 2).

Eighty-four larvae survived to adulthood, and 33 died either as a larva or as a pupa. Survival to adulthood was not random, since we found that larvae which had large signal size in the fourth instar were more likely to survive to adulthood (binary logistic regression, Wald = 4·470, $P = 0·035$). This difference was not due to size differences between the surviving and dead larvae (Wald = 0·609, $P = 0·435$). Diet had no effect on survival (Wald = 0·369, $P = 0·544$).

Discussion

If predator learning is a predominant factor in determining the warning signal architecture in aposematic animals, theoretical expectations imply directional selection to large signal size and thus reduced variation in signal expression (Müller 1879; Mallet & Singer 1987; Turner 1987; Endler 1991; Hagman & Forsman 2003; Beatty, Beirinckx & Sherratt 2004; Lindstedt *et al.* unpublished data). Contrary to this expectation, our study showed that *P. plantaginis* larvae have highly variable warning signal size (Fig. 1), and this variation has both a genetic and an environmental component. The larvae grown on *Rumex* had significantly larger signal size than larvae grown on artificial diet, suggesting that the colour formation can be plastic. Furthermore, we found that the larvae with a small orange patch, and thus were more black, developed slowly (Fig. 2) and were more likely to die before reaching adulthood. This could suggest that producing a black melanin pigment is costly and that larvae have to trade-off their growth and survival for maintaining melanin production (see also Windig 1999; Talloen, Van Dyck & Lens 2004). In *P. plantaginis*, the cost of slow growth decreases the chance of producing a second generation in a season. Moreover, slow growth can increase the risk of a larva becoming parasitized (Teder & Tammaru 2001). All this leads to a question: why do all larvae not have a large orange patch if this would result in a better avoidance by predators, and is less costly to produce?

We can suggest three hypotheses to explain why all individuals do not have large signal expression: (i) genetic correlations between signal size and life-history traits; (ii) high costs of conspicuousness and (iii) selection for signal size by predation is either weak or it varies in space and/or time.

First, the development time and signal size can be genetically correlated. Unfortunately, our sample size was not large enough to estimate reliably the genetic correlation between growth rate and signal size. However, there was a significant negative correlation calculated from family means between development time and signal size in the last instar; the larvae with a short development time also had a large signal and the families with high mean development time had larvae with large warning signals (Fig. 2). This suggests that a genetic correlation between these traits is likely. If this is true, it can help us understand variation in signal size among individuals. Genetic correlation between these traits would mean that selection for either of the traits would also affect the other. Therefore, for example, if an environment favours larvae with dark colour because of thermoregulatory benefits, these larvae also have a long development time. However, we need more careful studies on the genetic basis of the warning signal before we can fully understand whether genetic correlation hypothesis can explain the variation in *P. plantaginis* signals.

Second, the large pattern orange signal makes the larvae very conspicuous and thus an easy target for the predators (see Lindstedt *et al.* unpublished data). Therefore, depending on the guild of predators (Endler & Mappes 2004), the most beneficial defence strategy in some environments might be a combination of a crypsis and an aposematism (see Tullberg *et al.* 2005). When there are lots of predators that have not learnt to avoid the signal or can overcome the defences (Endler & Mappes 2004; Mappes, Marples & Endler 2005), a small warning signal (i.e. more melanin coloration) would then be beneficial compared to a strong signal that is more visible from a distance (Lindstedt *et al.*, unpublished data). However, more studies are needed to address warning signal architecture and its fitness correlations before we can make straightforward conclusions about the 'high detection cost' hypothesis.

Third, selection pressures on larval colouration can vary in time and space. This can be due to variation in the demands for thermoregulatory ability or variable predation pressure. Seasonal variation in larval colour has been found in previous studies (Fields & McNeill 1988; Hazel 2002), suggesting different selection pressures among seasons. Dark colouration can be important during the autumn and spring when the larvae need to warm up quickly (Lindstedt *et al.* unpublished data), whereas in the warmer summer months, the dark colouration might not be so important or it could be even selected against, since it exposes the larva to the risk of overheating (Fields & McNeill 1988). Also, as predator selection pressure improves, warning signal effectiveness might not be as intensive as is often assumed (see Ruxton *et al.* 2004). Perhaps learning and generalization of predators allow variation in warning signal pattern as long as a signal is distinguishable from cryptic prey (Wallace 1867; Sherratt & Beatty 2003; Rowe, Lindström & Lyytinen 2004). This is supported by the study of Holloway, Gilbert & Brandt (2001) indicating a more relaxed selection for the colour pattern of aposematic species than for Batesian mimics.

The hypotheses presented here are not mutually exclusive; it seems likely that many or all of them play a part in causing variation in the warning signal of *P. plantaginis*. Although the variation in warning signals might seem paradoxical in the light of the theory of warning signals that is heavily based on taking only predation pressure (and mainly predator learning) as an explanatory factor (e.g. Ruxton *et al.* 2004), it is more likely to be the result of several selection pressures on the colouration of warningly coloured animals (Edmunds 1974; Mappes *et al.* 2005). Our results underline that in order to achieve a more realistic view of signalling theory, we need to assess the life-history of animals (see also Longson & Joss 2006) and take into account that various selection pressures act in concert on colouration.

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