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ORIGINAL PAPER

Identifying the ecological conditions that select for intermediate levels of aposematic signalling

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Abstract Chemically defended species often have conspicuous signals that warn potential predators of these defences. Recent evidence suggests that some such aposematic prey are not as conspicuous as possible, even though increased conspicuousness would bring additional anti-predator benefits. Here we present a simple model to explore the generality of these observations. Our model predicts that optimal fitness will often be achieved at an intermediate level of conspicuousness and not simply by maximising conspicuousness. This comes about because of the ubiquitous trade-off that increased conspicuousness has an ecological cost in increasing the encounter rate with predators, as well as a benefit in terms of enhancing learned aversion by predators of defended prey. However, importantly, we also predict that a small deviation away from maximal crypsis generally causes a decrease in fitness, even if a larger deviation would lead to an intermediate level of conspicuousness that maximises fitness. Hence, further consideration of whether intermediate levels of aposematism are as common in nature as predicted in this model will require consideration of the underlying evolution of appearance, and the plausibility of evolution across the fitness trough, from maximal crypsis to an intermediate level of aposematism.

Keywords Aposematism · Conspicuousness · Optimisation · Predation · Signalling and communication

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Introduction

Defended animals often advertise their repellent secondary defences to would-be predators with a conspicuous appearance, such as the yellow and black stripes of many wasp species. This conspicuous appearance, often termed an *aposematic signal*, is generally considered to reduce mortality from predation, since predators learn to avoid individuals that signal that they have this defence. This may happen through a number of different pathways: the conspicuous appearance may enhance speed of aversion learning of initially-naive predators: increasing learning, for example, by attracting predator attention and hence increasing encounter rates. Alternatively, bright warning colours may make each encounter itself more easily learnt, regardless of encounter rate (see review in Ruxton et al. 2004). Learning may also be enhanced if the conspicuous appearance of the prey type helps to distinguish individuals of that prey type from other prey types that may not be so aversive (Guilford 1992; Wallace 1867). Although much less studied, conspicuous appearance may also aid in the retention and retrieval of learned aversions (Roper and Redston 1987; Speed 2000).

Important recent empirical work (Tullberg et al. 2005) suggested that although aposematic prey are often considered to be highly conspicuous to humans, some aposematic prey are not apparently as conspicuous as possible, even though there is good empirical evidence that increased conspicuousness might be expected to bring additional anti-predator benefits. Further examples of species that are likely to have evolved intermediate levels of conspicuousness are discussed by Endler and Mappes (2004). Indeed, the whole question of what we might call the “conspicuousness spectrum” in relation to the evolutionary ecology of prey defence is beginning to be systematically investigated by empiricists with phylogenetic and experimental techniques (Chiari et al. 2004; Darst et al. 2006; Hagman and Forsman 2003; Santos et al. 2003; Siddiqi et al. 2004; Summers and Clough 2001; Vences et al. 2003).

An important line of theory is provided by Endler and Mappes (2004). In a series of models, these authors demonstrate that an intermediate level of investment in conspicuous signalling might be expected when a defended species is subject to predation from several species, some of which are responsive to the signal and some of which are not. Although Endler and Mappes present an important new idea, it is not currently clear whether the multiple-predator scenario that they have identified is the only condition that can give rise to intermediate levels of aposematism, or whether their scenario is simply an example from a wider set of conditions. The expectation of a wider set of conditions is suggested by two papers: Leimar et al. (1986) and Speed and Ruxton (2007). Both these papers present models of the co-evolution of investment in defence and investment in signalling of that defence.

One explanation for diversity in warning signal strength is economic: there may be additional physiological costs associated with the production and maintenance of enhanced conspicuousness (Speed and Ruxton 2007). If these costs are not always matched by sufficient additional anti-predatory benefits, then the optimal level of conspicuousness will be less than the maximum possible. There is relatively little published work which demonstrates that conspicuous colouration may be costly either in proximate physiological terms, or in terms of direct fitness correlates. A good example, however, was recently reported by Ohsaki (2005) who demonstrated that the expression of bright mimicry patterns in the Batesian mimetic butterfly, *Papilio polytes*, is associated with decreased longevity in captive animals (Speed and Ruxton 2007, outline other studies which demonstrate or strongly imply that displays can be costly).

Thus, there might generally be a case of diminishing returns (in terms of reduction in predation risk) with increasing physiological investment in conspicuousness. This possibility has been modelled by Speed and Ruxton (2007), who showed that changes in physiological costs of displays, and of repellent secondary defences can predict a wide spectrum of conspicuousness levels between prey populations. However, the generality of these results could not be evaluated because the complexity of the model prevented analytic treatment and required evaluation of the model by numerical simulation. Furthermore, whilst plausible, the generality of this "economic" explanation cannot, however, be comprehensively evaluated with our currently limited understanding of the physiological costs of pigmentation. This leads us to ask whether optimal aposematic displays can be of intermediate conspicuousness for reasons other than predator mixes (Endler and Mappes 2004) or economic costs of production (Speed and Ruxton 2007).

The model of Leimar et al. (1986 and also the elegant model of Engen et al. 1986) considered learning as a key means by which aposematism could enhance survival. Leimar et al they sum up a general explanation for variation in aposematic display like this: "it seems inevitable that, as the coloration becomes brighter a point is reached where gain of higher rate of learning diminishes. An aposematic ESS will be located where the gain has diminished to a level that balances the increase in detection rate." However, the generality of their prediction is currently difficult to evaluate, since (as the authors themselves acknowledge) their model is too complex for a full evaluation of its predictions, never mind an evaluation of the sensitivity of these predictions to the values given to parameters. In this paper, we will present a much simpler model, that still captures the essential trade-off alluded to above, but which allows much more explicit and exhaustive study of model predictions. We focus on finding a general solution, inspired by the work of Leimar et al. (1986) based only on some widely acknowledged fundamentals of predator behaviour (i.e. that conspicuousness invites predatory attention, and that conspicuousness and secondary defences tend to aid survival during exposure to predation).

Given that intermediate aposematism may be explained without the need for predator mixes, or varied costs of display, the key purpose of this paper is therefore to explore the generality of the prediction of Leimar et al. (1986) that some non-cryptic form of aposematic display will not be as conspicuous as physiologically possible. We further aim to identify in the broadest terms the ecological conditions that are necessary for the observation of intermediate levels of aposematic signalling. That is, we are interested in identifying situations where prey neither express aposematic signalling minimally (i.e. being maximally cryptic) nor do they invest as fully in aposematic signalling as is physiologically possible for them. We do this under the challenging assumption that signals involve no physiological cost, and so maximal signalling can only be opposed by ecological disadvantages.

A simple model

There may well be ecological disadvantages to conspicuous appearance. By definition, more conspicuous individuals are more easily detected by other organisms in their environment. Thus, it seems reasonable to expect that the rate (E) at which individuals of a given prey type are encountered by potential predators is likely to increase (or certainly not decrease) with increasing conspicuousness (C). We assume that conspicuousness is described by a single parameter C, with C equal to zero indicating minimal possible conspicuousness (maximum crypsis) and increasingly positive C indicating increasing conspicuousness. We do not, however, assume that all encounters with potential predators lead to the death of the prey. Indeed, the general understanding of aposematic signals is that such signals decrease the likelihood of encounters with predators leading to death. It might be expected that (through innate avoidance, or learned avoidance, or differentiation from cryptic, undefended prey) increasing conspicuous leads to a reduction in the probability (P) that an encounter with a predator leads to the death of the prey individual.

Let us assume that a reasonable surrogate for fitness is the probability (S) of surviving a given period of time (T). This might be a day, or a season; for our purposes here, it is simply a constant period of time. From our definitions above and assuming that encounters with a predator occur as a Poisson process with mean $E(C)$, we can decompose this fitness surrogate:

$$S(C) = \exp(-E(C)P(C)T) \tag{1}$$

We are interested in situations where the maximum fitness does not occur when conspicuousness is either maximised or minimised. That is, S is maximised at some value of C that is neither 0 or ∞. Let us call this value $C = c$. A necessary condition for this to occur is that the function S has a turning point at c:

$$\left.\frac{dS}{dC}\right|_{C=c} = 0 \tag{2}$$

By simple calculus, this requires that

$$\left.\left(E\frac{dP}{dC} + P\frac{dE}{dC}\right)\right|_{C=c} = 0 \tag{3}$$

(Note that for fitness to be maximised at the minimum level of conspicuousness, C = 0, the expression in (3) must be negative at C = 0). Since, the first term in equation. (3) is always negative and the second is positive, and both will change in magnitude (potentially at different rates) with change in conspicuousness, then such an intermediate optimum is possible, depending on the specific functional forms of E & P. To make further progress we must choose specific forms.

Let us scale conspicuousness (C) such that $C = 0$ represents minimal conspicuousness, and $C = 10$ represents very high levels of conspicuousness. We will assume that even at minimal conspicuousness there is some possibility of being encountered by predators $E_{\min}$. We assume that E increases with increasing C, but saturates at a maximum value $E_{\max}$ according to the relation

$$E(C) = E_{\min} + (E_{\max} - E_{\min})(1 - \exp(-\varepsilon C)),$$

where ε controls the rate of increase in E with increasing C. Let us imagine the focal species to be the larvae of a butterfly that lives as a caterpillar for a period of 30 days, so $T = 30$. For a maximally cryptic individual, the probability of being encountered at least once in this time is given by

$$1 - \exp(-30E_{\min})$$

If we assume that this probability is 0.5, then this gives a value for $E_{\min}$ of 0.023. Let us further assume that maximal conspicuousness increases encounter rate fifty fold, so that $E_{\max} = 50E_{\min}$. If we assume that ε is 0.5, then E will have increased over 92% of its possible range ($E_{\max} - E_{\min}$) as C increases from 0 to 5, and 99.3% by $C = 10$.

We assume that the focal prey is in some way defended or otherwise unattractive to predators, hence predators find consuming a prey individual to be an aversive experience. It may be that even in the absence of any learning through aposematic signalling (i.e. when $C = 0$), the prey has some chance of surviving an attack, because its aversiveness is indicated prior to consumption. This may be small, because even if the predator rejects the prey without consuming it, the process of prey capture and subsequent handling may well mortally injure the prey.

Let us assume that the probability of a maximally cryptic prey being killed as a result of a single encounter with a predator, $P(0) = P_{\max} = 0.975$, giving this maximally cryptic prey a 2.5% chance of surviving a single encounter. We expect P to decrease with increasing C, but again for this to saturate. It is well established that predators behave more warily with respect to prey with toxins and aposematic signals than with respect to prey with non-aposematic appearances (e.g. Gamberale-Stille 2000; Gamberale-Stille 2001; e.g. Gamberale and Tullberg 1996; Gamberale and Tullberg 1998; Kelly and Marples 2004; Schuler and Roper 1992; Sillén-Tullberg 1985; Skelhorn and Rowe 2006a; Skelhorn and Rowe 2006b). In addition, it is well established that avoidance learning is enhanced with conspicuous, rather than cryptic appearances (Gittleman and Harvey 1980; Roper and Redston 1987). Thus, we could represent $P(C)$ by

$$P(C) = P_{\min} + (P_{\max} - P_{\min}) \exp(-\varphi C).$$

Even if predators learn to completely avoid prey, there will still be some mortality during the learning process, so let us assume $P_{\min}$ to be 0.025, so for maximally conspicuous prey there is only a 2.5% chance of an encounter with a predator leading to its death.

One can imagine however that more conspicuous prey can be detected by predators from greater and greater distances, however the added conspicuousness is unlikely to continue to make the prey more memorable or more distinct from alternative prey types. Thus, it is probably reasonable to expect that the survival benefits of increased conspicuousness will saturate more quickly (with increasing conspicuousness) than the encounter-rate costs and so $\phi > \varepsilon$. Thus, let us assume $\phi = 10\varepsilon$.

Model predictions

With the default parameter values introduced above, the relationship between survival and conspicuousness is as shown in Fig. 1. We find that survival is maximised at an intermediate value of conspicuous ($C \sim 1$), for these parameter values. However, this will not always be the case depending on parameter values. If we define $E_{\max} = \alpha E_{\min}$ and $P_{\max} = \beta P_{\min}$ then it is easy to see that the value of C that optimises S will be independent of $E_{\min}$ and $P_{\min}$ (and T) and dependent only on α, β, ε and ϕ. From above our default values are $\alpha = 50$ and $\beta = 39$, $\varepsilon = 0.5$ and $\phi = 10\varepsilon$.

Using these definitions, we can evaluate (3) at $C = 0$ to get:

$$\varepsilon\beta(\alpha - 1) - \phi(\beta - 1),$$

for our default parameters, this is positive and so fitness declines as C increases from zero. If α and β are both substantially bigger than one (i.e. conspicuousness has large effects on both encounter rates with predators and likelihood of surviving encounters) then this will be true, to a reasonable approximation, providing $\alpha > (\phi/\varepsilon)$. We expect this to be true for natural situations, and so in general we would expect that if the value of C that maximises

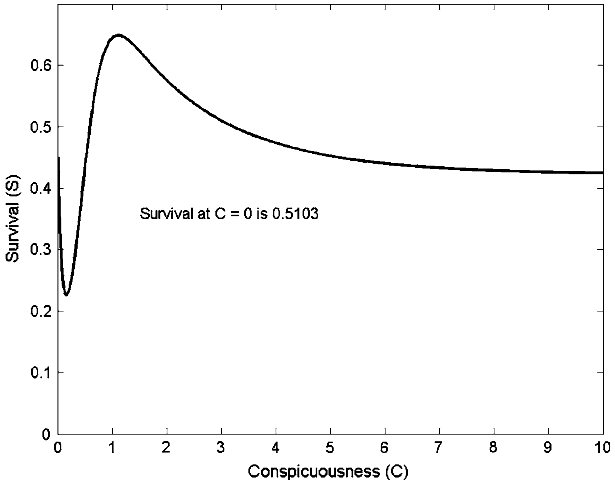

Fig. 1 The relationship between survival and conspicuousness for the default parameter values

fitness is non-zero, then reaching that level of conspicuousness may involve spanning the fitness valley of conspicuousness values just slightly greater than zero.

Sensitivity of model predictions to specific parameter values

We have shown in Fig. 1, that our default parameter values predict that fitness is optimised by an intermediate (rather than an extreme) value of conspicuousness. Let us now evaluate fitness for a range of parameter values to explore the generality of this result. First, let us consider variation in α and β. In principle, α can take any value greater than or equal to one, with increasing values of α indicating that encounter rate with predators can rise to higher values (providing conspicuousness is high enough). Since P is a probability, β values are restricted such that P must be bounded above by one, thus (for our default value of $P_{\min}$ of 0.025), β is restricted to take values between 1 and 40.

Consideration of Fig. 2a shows that intermediate optima are predicted over a wide range of α and β values. The solid line shows the effect of variation in β for the default value of α. As you would expect, increasing α increases the optimal conspicuousness value, but this effect is relatively unspectacular over a wide range of β values: $23 < \beta < 40$. However, if β falls below a critical value, then there is a step change, with the intermediate optima disappearing and fitness being maximised when conspicuousness is minimised. As can be seen from the dashed and dotted lines: increasing α moves this threshold value of β higher. Hence we conclude that an intermediate value for optimal conspicuousness is commonly predicted by our model providing β is sufficiently high and α is not too high. This makes intuitive sense, since a large value of β indicates that there is significant advantage to be gained from high conspicuousness in terms of the risk of death in a single encounter, and a small value of α indicates that there is less of a cost to high conspicuousness in terms of increased encounter rate.

Let us turn to the other two parameters that can affect the optimal level of conspicuousness: ε and ϕ. Again, Fig. 2b suggests that intermediate levels of aposematism are predicted over a wide range of values for these model parameters. We define a further variable ρ, which is the ratio (ϕ/ε). We see that when this ratio is low, then the optimal

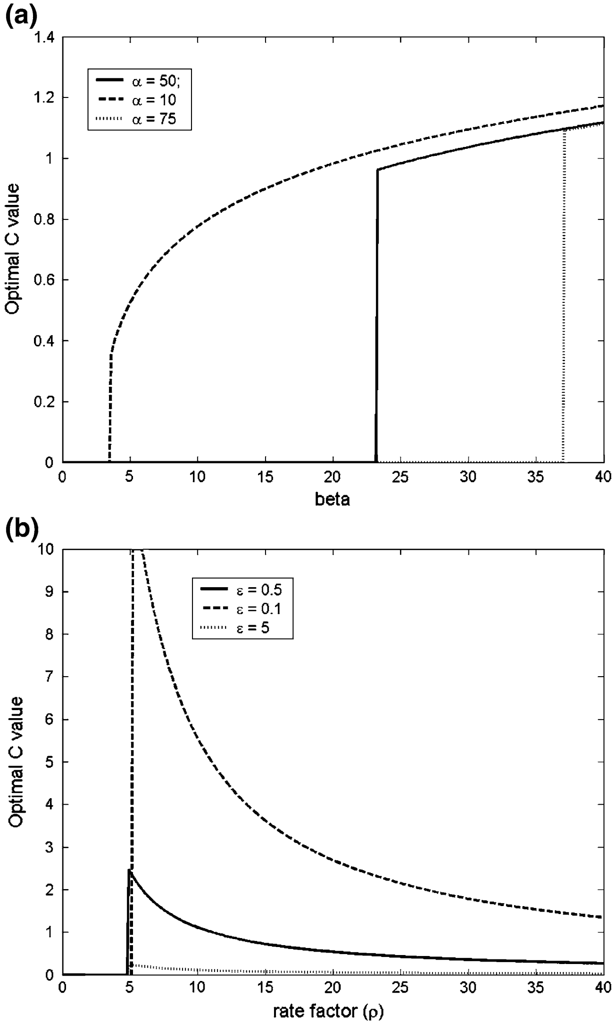

Fig. 2 (**a**) The value of conspicuousness that maximises fitness. All parameters take their default values except α and β. (**b**) The value of conspicuousness that maximises fitness. All parameters take their default values except ε and ϕ. ϕ is given by ε multiplied by the rate factor ρ

strategy is to minimise conspicuousness. This makes sense since a low ratio would suggest that the cost of conspicuousness (*E*) rises more quickly with increasing conspicuousness, than the benefit (*P*). However, once a threshold in this ratio is exceeded there is a dramatic step change, with high conspicuousness now being optimal. If ε is small (e.g. the dashed line in Fig. 2b) then this optimal value of conspicuousness can be very high. However, regardless of the value of ε, the optimal value of conspicuousness declines with further increases in the ratio. Again, this makes sense, since for a high ratio, the benefits (*P*) of increased conspicuousness saturate quickly, and further increases in conspicuousness affect the costs (*E*) more than the benefits. Thus, we conclude that our model readily predicts intermediate levels of conspicuousness to be optimal provided that the benefits of conspicuousness accrue considerably more rapidly with increasing conspicuousness than the costs do (i.e. ρ is higher than some threshold) and that the effect of increasing conspicuousness on encounter rate with predators is sufficiently high (ε is above some threshold).

Discussion

Our model predicts that optimal fitness will often be achieved with an intermediate level of conspicuousness and not simply by maximising conspicuousness. Hence the observation of Tullberg et al. (2005) that the appearance of a caterpillar species appears to be neither as conspicuous as possible nor as cryptic as possible is entirely in accord with our model predictions. Indeed our model predicts that such intermediate appearances should be the rule in the natural world. Of course, model predictions are only of interest if the model assumptions are valid. However, as we discussed when presenting our model, its simple structure utilises a small number of explicit assumptions that are generally well supported both logically and empirically. Also, we must bear in mind that the conclusion of Fig. 1 that generally a small deviation away from maximal crypsis causes a decrease in fitness in our model, even if a larger deviation would lead to an intermediate level of conspicuousness that maximises fitness (see also the models of Engen et al. 1986; Speed and Ruxton 2007). Hence, further consideration of whether intermediate levels of aposematism are as common in nature as predicted in this model will require consideration of the underlying evolution of appearance, and the plausibility of crossing the fitness trough, from maximal crypsis to an intermediates level of aposematism (Mallet and Singer 1987). However, the abundant examples of aposematism provided by the natural world do suggest that evolution away from maximal crypsis is certainly possible. It is worth remembering that a move away from crypsis may not require a change in the intrinsic appearance of the organism, it may involve a change in behaviour or in microhabitat. For example, an organism that switches from being nocturnal to diurnal may dramatically change its exposure to predators (Merilaita and Tullberg 2005) Similarly, if a butterfly changes the plant that it lays its eggs on, this may have a dramatic effect on the level of crypsis experienced by the eggs. More generally, understanding evolution away from crypsis should not be thought of necessarily requiring a macromutation causing a step-change in intrinsic appearance, but is likely to involve complex interplay of phenotype and environment. The plausibility of evolution away from crypsis by the accumulation of small changes in intrinsic appearance is not fully resolved. In a particularly interesting set of experiments, Lindstrom et al. (1999) present evidence that slight deviations from optimal crypsis did not suffer from the enhanced exposure to predators assumed in our model; further empirical and theoretical exploration of this is very much warranted. Notice that the fitness trough considered here occurs through a different mechanism to the commonly acknowledged challenge of how an initial conspicuous mutant is prospers when the benefits of aposematism are density-dependent.

This issue of density dependence is not considered in our model, and various explanations for how this density-dependent effect can be overcome are discussed in Ruxton et al. (2004). By comparing the fitness of individuals in implicitly monomorphic populations, our model allows us to comment on the ecological situations that might be associated with different strategies of expression of conspicuousness, and particularly to shed light on the mechanisms involved in relating ecological factors to conspicuousness. It was not our intention to provide detailed consideration of the evolutionary path by which such strategies might be reached. In studying the evolution of level of conspicuousness, it would also be important to consider than both the rate at which an individual of given conspicuousness was encountered by predators (E in the model) and the outcome of each encounter (P in the model) could be influenced by the frequency of that phenotype in the environment and by the nature of the other phenotypes present in the population. If an individual is of a rare phenotype then this may reduce its rate of encounter with predators that have not formed a search image for that phenotype. The outcome of the encounter might also be affected by frequency-dependent effects. The predator may decline to attack uncommon prey because of some neophobic mechanism. Further, warning signals are generally considered to require predators to generalise from past experiences with similar looking prey, so the avoidance of a given prey individual will be intrinsically linked to the appearances of those prey that the predator has recently experienced. Hence, although we have kept the model used in this paper as simple as possible (for example, implicitly assuming a monomorphic prey population), in order to identify and isolate the key processes at work, further theoretical development will require necessarily more complex models. This will require a change in modelling from simple optimisation to a game theory approach that allows frequency-dependent effects to be fully considered.

It is important to remember that the mechanism demonstrated here to produce intermediate levels of aposematic signalling could potentially work alongside previously-discussed mechanisms. That is, if a species if found to display intermediate aposematism, then this could be for any combination of the three mechanisms that have now been considered to produce this effect. These three mechanisms are the trade-off between encounter-rate and predators' attack decisions discussed here, a trade-off between ecological benefits of enhanced signalling and physiological costs and a trade-off induced by a balance of different potential predators only some of which are responsive to aposematic signals. The relative importance of the mechanisms in a particular case will require empirical determination. The most obvious experiment is to manipulate individuals of the focal prey type to either enhance or reduce the aposematic signal, and observe the consequences of these manipulations on the behaviour of predators. Measuring physiological costs of signalling is methodologically challenging, but the most straightforward experiment is to restrict the food intake of individuals of focal species and explore how such restriction impacts of strength of signalling. Whilst such experiments can probe whether each of the three mechanisms appears to contribute or not, if more than one appears to contribute then estimation of the relative importance of each to the final signal strength will require very careful and involved exploration.

The models of Endler and Mappes (2004) were very important in demonstrating that intermediate levels of conspicuousness can be selected for. Here we have not only confirmed this prediction using a model with a different set of assumptions, but suggested that the occurrence of intermediate levels of conspicuousness may be even more common in the natural world than suggested by previous works. Indeed, we predict that aposematic signals in general will not be as conspicuous as physiologically possible, even if more conspicuous signals could be achieved at no physiological cost. This comes about because of the ubiquitous trade-off involved in aposematism, that increased conspicuousness has an ecological cost in increasing encounter rate with predators, as well as a benefit in terms of enhancing learned aversion of defended prey.

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