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Citation: Broom, M., Speed, M. P. & Ruxton, G. D. (2006). Evolutionarily stable defence and signalling of that defence. Journal of Theoretical Biology, 242(1), pp. 32-43. doi: 10.1016/j.jtbi.2006.01.032

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Link to published version: https://doi.org/10.1016/j.jtbi.2006.01.032

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Evolutionarily stable defence and signalling of that defence

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Key words: conspicuousness, crypsis, secondary defence, ESS, predator, prey

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Abstract

We examine the evolution and maintenance of defence and conspicuousness in prey species using a game theoretic model. In contrast to previous works, predators can raise as well as lower their attack probabilities as a consequence of encountering moderately defended prey. Our model predicts four distinct possibilities for ESSs featuring maximum crypsis. Namely that such a solution can exist with (1) zero toxicity, (2) a non-zero but non-aversive level of toxicity, (3) a high, aversive level of toxicity or (4) that no such maximally cryptic solution exists. Maximally cryptic prey may still invest in toxins, because of the increased chance of surviving an attack (should they be discovered) that comes from having toxins. The toxin load of maximally cryptic prey may be sufficiently strong that the predators will find them aversive, and seek to avoid similar looking prey in future. However, this aversiveness does not always necessarily trigger aposematic signalling, and highly toxic prey can still be maximally cryptic, because the increased initial rate of attack from becoming more conspicuous is not necessarily always compensated for by increased avoidance of aversive prey by predators. In other circumstances, the optimal toxin load may be insufficient to generate aversion but still be non-zero (because it increases survival), and in yet other circumstances, it is optimal to make no investment in toxins at all. The model also predicts ESSs where the prey are highly defended and aversive and where this defence is advertised at a cost of increased conspicuousness to predators. In many circumstances there is an infinite array of these aposematic ESSs, where the precise appearance is unimportant as long as it is highly visible and shared by all members of the population. Yet another class of solutions is possible where there is strong between-individual variation in appearance between conspicuous, poorly defended prey.

Secondary defences increase the inclusive fitness of a prey animal by increasing the likelihood that it escapes from a predator without serious injury and/or by decreasing the probability that the same predator will attack the prey and its relatives in the future. Though diverse in form, components of secondary defences can be broadly classified into locomotor (rapid escape, protean evasive flight), morphological (spines, tough integuments etc.) and chemical (toxins, venoms, noxious secretions etc.) classes. In some cases defences may be visually detectable before an attack is launched and function as their own reliable signal to predators; the existence of numerous sharp spines or the mode of locomotion of an animal may present predators with reliable and detectable cues as to the unprofitability of specific prey types.

In many other cases, and especially in examples of chemical defences, the threat posed by secondary defences are not easily evaluated by potential predators using external cues in prey; here defended prey "*require some signal or danger flag which shall serve as a warning to would-be enemies not to attack them, and they have usually obtained this in the form of conspicuous or brilliant coloration, very distinct from the protective tints of the defenceless animals allied to them"* (p. 232, Wallace, 1889).

Thus many, but not all, prey with effective secondary defences possess danger flags in the form of more or less conspicuous ("aposematic") warning displays that help predators distinguish edible from unprofitable and dangerous species.

Given that defended prey can vary their degree of conspicuousness, a pertinent question is *how conspicuous* (or how cryptic) should a particular prey be? Conspicuousness is, in many prey, directly traded-off against crypsis, such that the benefits that accrue from conspicuousness (reduced recognition errors, enhanced wariness, accelerated learning and decelerated forgetting processes in predators) are gained at the expense of increased rates of detection by predators. Should we expect optimal conspicuousness to increase continuously with the strength of a prey animal's defence, as has recently been suggested (Summers & Clough, 2001), or can we expect a more complex relationship between defence and conspicuousness? A second, related and important question is; whether (and when) should defended prey show between-individual variation in their appearance.

Defences themselves may be costly and therefore be traded-off against other components of fitness. There is a growing body of empirical literature that demonstrates that many chemical defences incur fitness costs, either through the costs of biosynthesis or acquisition (via sequestration or symbiosis) and storage. Such costs are often seen in reductions in growth, in adult size, in fecundity or have been directly measured in energetic terms (Cohen, 1985; Zalucki et al., 2001; Bowers & Collinge, 1992; Camara, 1997; Bjorkman & Larsson, 1991; Rowell-Rahier & Pasteels, 1986; Dobler & Rowell-Rahier, 1994; Grill & Moore, 1998), although we note that in some circumstances costs have not been detected (Bowers, 1988; Kearsley & Whitham, 1992). Another pertinent question is therefore "*how much should any given prey invest in its defences?"*

To date the co-evolution and optimisation of constitutive defences in prey animals and signals of those defences have received surprisingly little theoretical attention. The model of Leimar et al. (1986) is, however, particularly important. This model includes: (1) components of an individual predator's psychology and behaviour (varied learning rates and sensory generalisation in order to calculate attack probabilities); (2) the properties of individual prey (continuous variation in effectiveness of unprofitability in terms of individual survival and effects on predators' learning rates, costs of a defence, and degree of conspicuousness) and (3) structuring of prey populations (size and degree of clustering of prey as a proxy for kin selection). Leimar et al. combine these components into a model that determined evolutionarily stable strategies (ESSs) for the continuously-varying parameters of conspicuousness and unprofitability. Their model predicts that there can be a single monotypic ESS for some nontrivial level of defence for a prey of given conspicuousness. Increases in optimal levels of defence would be caused by: (i) increases in survival rates of individuals combined with (ii) a positive relationship between learning rate and prey unprofitability provided that there was a capacity for predators to confer the benefit of avoidance learning on the same individuals (through repeated attacks) or through kin grouping.

Furthermore, Leimar et al. (1986) found that kin grouping, perhaps combined with an increase in predation threat, could destabilise crypsis in favour of aposematism, but that, once evolved, kin grouping was not necessary for the maintenance of aposematism. When aposematism already exists, it could be stabilised by (i) a positive relationship between conspicuousness and learning and (ii) a supernormal (or peak-shift-like) response, in which the strongest levels of avoidance are

conferred on phenotypes that are more conspicuous than those generally encountered. The game theoretic approach developed by Leimar et al. represents a seminal work in the theory of prey defences and warning signals, providing a framework in which the evolution of both traits can be analysed. However we note a number of areas that in our view warrant further attention and development.

The model of Leimar et al. (1986) considers a set of naïve predators (initially one individual) that start out with an initial "excitatory" attack tendency described as $e(x)$, its generalisation gradient due to the "*predator's experience of cryptic and profitable prey of other species*". When these naïve predators now meet unprofitable prey, generalised attack probabilities are reduced according to an inhibitory gradient $h(x,x_1,y_1)$, where x_1 is the conspicuousness and y_1 the unprofitability of the encountered prey individual. Hence, in this model, attack probabilities for a range of prey appearances are determined by a generalisation function of the form

$G(x) = e(x)[1- h(x,x_1,y_1)]^n$ where n is the number of previous encounters between predator and prey.

Since the model of Leimar et al. (1986) was constructed to explicitly examine the effects of individual predator psychology on aposematic evolution, this formulation is entirely reasonable. However, the implication of this component of the model is that the predator can reduce its range of generalised attack probabilities, because of repeated inhibitory effects, but it cannot ever raise it. Whichever prey gets attacked, whatever their appearance and toxicity, whatever the outcome, the aversion of the predator increases for every further prey individual encountered, or at least cannot decrease. However, this is clearly not an appropriate long-term strategy for a predator, as it must necessarily lead to ever decreasing uptake rates. In addition, we argue in this paper that the generality of the results described in Leimar et al. (1986) can in some cases be hard to evaluate, as they select specific functional forms at the outset. A more general model of predation may provide a more flexible framework for evaluation.

In this paper we therefore examine the evolution of conspicuousness and defence in defended species with a complementary model to that of Leimar et al. (1986). We assume that the secondary

defence is a form of toxicity (though it can clearly be extended beyond this) and present a model that we strive to make as general as possible whilst still being capable of making useful specific predictions. Thus, rather than describe the effects of learning in individual predators, a set of predators is modelled here as a group in equilibrium for states of learning, hunger etc.

Furthermore, in the model described here, predators can both lower and raise their attack probabilities with prey that contain modest quantities of toxins (Sherratt et al., 2004). We use the model to investigate (1) the relationship between defence and the appearance of a prey when the levels of mortality from causes other than predation and the degree of kin grouping varies; (2) the optimal level of conspicuousness for a range of toxicity levels; and (3) the extent to which optimal toxicity can be affected by the appearance of an animal and the degree of kin grouping within the population.

Model Description

We consider a single population of individuals that are potentially prey to a predator. Each prey individual i is described by three parameters $\{t_i, r_i, \theta_i\}$. The parameter t_i describes the toxicity (or, more generally, investment in anti-predatory defence) of individual i, with increasing values indicating increasing toxicity, and $t_i = 0$ indicating minimal investment in toxicity. The parameter r_i describes the conspicuousness of individual i (or more generally the probability of detection upon encounter with a predator is an increasing function of r_i). Increasing values of r_i indicate increasing conspicuousness, with $r = 0$ indicating maximum crypsis. The final parameter θ_i also describes the appearance of the individual, but such that changes in θ affect the appearance of the individual without affecting its conspicuousness. Thus two prey types can be equal in conspicuousness against the background (have identical r values) but be very different in appearance from each other (have different θ values). For example two brightly coloured butterfly species can be equally easy to detect against the background foliage but can still be identified as distinct species. . Thus r and θ are orthogonal axes that together describe the parameter space of possible appearance. Without loss of generality, we assume that these axes are polar rather than Cartesian, θ taking values in $(0,2\pi)$. We are interested in finding the evolutionary stable values of $\{t_i, r_i, \theta_i\}$.

A key assumption of the model is that toxin production is expensive. We describe this by assuming that the fecundity of an individual F is a decreasing function of t_i. However, there is also a direct benefit to toxicity in that increasing investment in toxicity increases the likelihood of surviving a predatory attack. Specifically, we assume that if the predator attacks a prey item then the probability that the prey is captured (K) is a declining function of t.

There is another way that toxicity can affect survivorship and this is by influencing the probability that upon encountering an individual prey item, the predator decides to attack that particular prey individual. This probability (denoted by Q) declines with the aversiveness of the experiences that the predator is likely to have previously had (and subsequently remembered) on attacking similar looking prey items. Let us consider a predator attacking individual i. We first of all need to define "similar looking" individuals to individual i. We do this with a function $S(r_i,\theta_i, r_j, \theta_j)$, which is a measure of the visual similarity between individuals i and j. S increases as the points $\{r_i,\theta_i\}$ and $\{r_j,\theta_j\}$ get closer together; in particular in this paper we treat S as a univariate function of the Euclidian distance between the two species (see Appendix 1). We also have to describe the aversiveness of an experience with a prey item, which we do with function H. Specifically $H(t_j)$ is the aversiveness of attacking individual j. Positive values of H indicate an aversive experience; the higher the toxicity, the more positive H is and so the more aversive the experience. However, if an individual's investment in toxins is low then the experience of attacking it may not be aversive at all, indeed the predator may treat it as a beneficial experience. We describe such situations by a negative value of H. We define the critical value of toxicity (t_c) as that which produces a neutrally aversive response:

$$H(t_c) = 0 \qquad (1)$$

This non-zero value of t_c represents the phenomenon that prey may have to invest non-trivially in defence to become sufficiently aversive as to be unattractive to predator. That is, predators may be prepared to still consume prey with some mild aversive features, because the rewards of nutritional content are worth this small cost. We also need to describe encounter rates between the predator and prey, and the ease with which they are subsequently remembered. We assume that the probability that an individual of conspicuousness r is detected by a predator when it encounters

it is D, where D is an increasing function of r but even maximally cryptic prey have some chance of being detected (i.e. when $r=0$, $D(r)>0$). The rate at which such encounters occur and are later recalled by the predator is L, where L too is an increasing function of r. If the predator has perfect recollection of all encounters then $L = D$. Drawing all this together, on encountering individual i, then the available information to the predators (scaled by the total number of predators) on the attractiveness or aversiveness of that prey item (denoted I_i) can be calculated as follows

$$I_i = \frac{1}{n} \sum_{j=1, j\neq i}^{N} L(r_j) H(t_j) S(r_i, \theta_i, r_j, \theta_j) \qquad (2)$$

where N is the number of prey items in the population and n is the number of predators. We shall take this as our measure of the information that an average predator has about individual i. When this individual meets a predator, we assume that it is equally likely to be any of the n available, so that the predator will on average have this information about its aversiveness. It shall be further assumed that the population is in equilibrium, and its size is sufficiently large, so that any individual encounter has no effect on the population size. We assume that on encountering individual i, the probability of the predator mounting an attack is $Q(I_i)$ and Q declines with increasing I_i.

We must now describe the fitness of individual i. We assume that there is a background mortality rate λ. From our arguments above, the rate of predator-induced mortality on this individual, assuming without loss of generality that any prey individual encounters a predator at unit rate, is $D(r_i)K(t_i)Q(I_i)$, and so the fitness of individual i can be described by

$$\frac{F(t_i)}{\lambda + D(r_i)K(t_i)Q(I_i)}.$$

It is this fitness function that we use in our ESS calculations, where we consider inclusive fitness assuming that the average relatedness between individuals is a. Note, since we are only interested in situations where the population is at equilibrium, this fitness description is equivalent to the

alternative per capita rate of increase. Our ESS calculations are outlined in Appendix 1, and the key results presented in the next section. It should be noted at this point that a strategy which can be attained through small, selectively advantageous steps is called convergence stable. We only demonstrate when strategies in our model are resistant to such changes, and do not show that strategies are convergence stable.

Results

We explore the different types of ESS possible in our model in this section. We break this down by considering the different types of conspicuousness (r_1) in turn. For each such appearance there is an optimal level of toxicity (t_1) given by the function

$$g_1(r_1,t_1)=\left(\frac{\lambda+D(r_1)K(t_1)Q(I_1)}{D(r_1)K(t_1)Q(I_1)}\frac{F'(t_1)}{F(t_1)}-\frac{K'(t_1)}{K(t_1)}-aI_1\frac{Q'(I_1)}{Q(I_1)}\frac{H'(t_1)}{H(t_1)}\right)=0 \qquad (3)$$

provided that this yields a non-zero toxicity, where the information of toxicity is given by

$$I_1=\left(\frac{N-1}{n}\right)L(r_1)H(t_1)\approx\left(\frac{N}{n}\right)L(r_1)H(t_1) \qquad (4)$$

since N is large.

i) ESS featuring maximal crypsis (i.e. r = 0)

Appendix 1 demonstrates that there will be an ESS with $r = 0$, if and only if we satisfy the condition:

$$\frac{D'(0)}{D(0)}+I_1\frac{Q'(I_1)}{Q(I_1)}\left(S'(0)(1-a)+a\frac{L'(0)}{L(0)}\right)>0 \qquad (5)$$

where we represent the average relatedness of individuals in the "local" area by *a,*

$I_1 = \left(\frac{N}{n}\right) L(0) H(t_1)$, and t_1 is the ESS level of toxicity, which is found by substituting $r_1 = 0$ in equation (3).

Note that it is also possible for $t_1 = 0$ to be stable, which occurs if

$$g_1(0,0) < 0 \qquad (6)$$

This set of equations can only be solved iteratively once specific functional forms for all the functions and all parameter values have been specified. But the results in Appendix 1 do allow us to draw general conclusions about the type of maximally cryptic ESSs that are possible. Specifically, there is an ESS with maximum crypsis and minimal investment in toxins (i.e. $r = 0$, $t = 0$) provided that inequalities (5) and (6) are satisfied.

However, it is also possible for the ESS to involve significant investment in toxins without this triggering a change from maximally cryptic appearance. That is, there is an ESS with ($r_1 = 0$ and $t_1 > 0$), if equation (3) and inequality (5) are satisfied.

ii) ESS with warning colouration (i.e. r > 0),

One result from Appendix 1 is that individuals will never give up on maximal crypsis unless there is investment in toxins. That is, there is never an ESS with $r_1 > 0$ and $t_1 = 0$. In fact, there is no ESS with $r_1 > 0$, unless the associated toxin investment is sufficiently strong to be aversive (i.e. $t_1 > t_c$). However an ESS with $r_1 > 0$ can exist providing that equation (3) is satisfied, together with

$$t_1 > t_c \qquad (7)$$

and

$$g_2(r_1, t_1) - g_3(r_1, t_1) < 0 \qquad (8)$$

where

$$g_2(r_1,t_1)=\left(\frac{D'(r_1)}{D(r_1)}+aI_1\frac{Q'(I_1)}{Q(I_1)}\frac{L'(r_1)}{L(r_1)}\right), \quad (9)$$

$$g_3(r_1,t_1)=\frac{Q'(I_1)}{Q(I_1)}S'(0)I_1(1-a), \quad (10)$$

However, an interesting aspect to this case, is that we demonstrate in Appendix 1 that when an ESS with warning colouration is possible, then there is no unique ESS, indeed, there is an infinite number of ESSs. Specifically, under reasonable conditions on the parameters, there will be a lower critical value of r (denoted R), and all values $r > R$, have a unique value of t such that $\{r,t(r)\}$ is an ESS. This critical value of R is given by

$$V(I_1)=-I_1\frac{Q'(I_1)}{Q(I_1)}=-\frac{D'(R)}{D(R)}\Big/\left(S'(0)(1-a)-a\frac{L'(R)}{L(R)}\right). \quad (11)$$

The value of $t(r)$ (obtained from equation (3)) always increases with increasing r, and so we predict a strong correlation between investment in toxicity and conspicuousness of aposematic signals.

iii) ESSs where there is heterogeneity in appearance between individuals.

For the ESSs that have been discussed so far, the value of θ has been irrelevant. For maximally cryptic solutions with $r = 0$, it is easy to see that there is no selection pressure on the value of θ. For the ESSs with aversive prey ($t_1 > t_c$) and warning colouration ($r > 0$), it is clear there is now strong selection pressure on θ, but this selection pressure drives the population towards homogeneity in this parameter, the final parameter value settled upon is irrelevant providing all individuals adopt the same value (i.e. all individuals look alike).

However, in Appendix 1 we demonstrate that there are situations where the prey contains no toxins or some moderate level of toxin but is not aversive in the sense that predators increase their willingness to attack similar looking prey in future ($t_1 < t_c$) where the solution is more complicated. Here, the evolutionarily stable appearance is not full crypsis (i.e. $r_1 > 0$). This is due to the fact that looking very similar to other non-toxic cryptic individuals outweighs the benefit of

the extra crypsis. Some "aposematic distinctiveness" (in the sense of A.R. Wallace's original formulation) from more edible prey types is therefore optimal, even though the prey is not outright aversive. Such a solution will only occur when a small decrease in crypsis (a small increase in r) does not cause a large increase in encounter rate ($D(r)$).

Discussion

We first consider the general classes of possible ESS solution and subsequently consider how variation in the value of key variables determines which solution(s) is most likely. Finally we compare the model described in this paper with the original model in Leimar et al. (1986).

Evolutionary stable outcomes

Our model predicts four distinct possibilities for a solution with maximum crypsis (r=0). Namely that (1) such a solution exists with zero toxicity (t=0), (2) it exists with a non-zero but non-aversive level of toxicity ($0<t<t_c$), (3) it exists with a high, aversive level of toxicity ($t>t_c$) or (4) that no such maximally cryptic solution exists. That is, under some, but not all circumstances, an ESS involving the prey all minimising the rate at which they are detected by predators occurs. Interestingly, maximally cryptic prey may still invest in toxins, because of the increased chance of surviving an attack that comes from having toxins. The toxin load of maximally cryptic prey may be sufficiently strong that the predators will find them aversive, and seek to avoid similar looking prey in future. However, this aversiveness does not necessarily trigger aposematic signalling, and highly toxic prey can still be maximally cryptic, because the increase in rate of attack from becoming more conspicuous is not necessarily always compensated for by increased avoidance of aversive prey by predators. In other circumstances, the optimal toxin load may be insufficient to generate aversion but still be non-zero (because it increases survival), and in yet other circumstances, it is optimal to make no investment in toxins at all.

Each of these four possibilities may (for some combinations of parameter values) exist as the only ESS (which we label as situation *a*). However there are also combinations of parameter values where each type of maximally cryptic ESS exists alongside a range of non-cryptic ESSs, which

involve aversive levels of toxins (we label such situations *b*). Any such non-cryptic solution is more stable the larger the information of the toxicity of that appearance (thus conditions are often given in terms of I_1 is greater than some value). Under reasonable conditions the solution pair *r,t(r)* are stable for values of *r* above a given threshold *R*, so that multiple (infinite) solutions exist in many circumstances. Effectively, if an animal is conspicuous enough to be easily seen and this indicates high toxicity so that predators avoid it, it does not matter exactly which level of conspicuousness the prey individuals choose as long as everyone looks the same.
Any animal that changes its appearance will suffer, so all levels of conspicuousness above a certain threshold are stable.

Higher levels of conspicuousness are generally associated with higher levels of toxicity. Thus there are eight distinct scenarios (1-4,a-b), between each of which we can specify (admittedly complex) boundary conditions in terms of the values given to parameter values.

Note that it is possible that there is no solution either with r=0 or r>0, where all individuals are identical in toxicity and appearance. In this case, the solution will have the population of prey individuals uniformly spread across all θ values. They need not all have identical *r* values, and in general will not. Generally we expect a critical maximum value of *r*, below which all prey select values. Again increasing *r* will be associated with increasing (or at least non-decreasing) toxicity. Such non-point solutions occur when prey seek to be different from others, to disrupt associative learning. In our model increased between-individual separation in appearance is associated with increased conspicuousness (and so increased attack rates). It is this trade-off between minimising attack rates and maximising visual difference from other prey that generates this heterogeneous-appearance ESS.

Key parameters and the nature of the ESS

Rather than solve our equations for specific cases of functional responses and parameter values, we can make general statements about the influence of our various parameters on which solutions are likely to occur. For any particular value of *r* there is a unique optimal value of toxicity *t*. In general for *r>0* the higher *t* is in conjunction with *r*, the more likely it is to be stable against

changes in appearance (higher t means higher I_1, see (4) and (5)). Increasing the level of deaths from other causes λ reduces the value of t for a given r, and so reduces the likelihood of the solution being stable, and reduces the stable range of non-cryptic solutions. This makes sense since, as the influence of predation declines, the value of deterrence declines relative to the decreased fecundity of higher toxicity. Increasing the level of relatedness a increases the toxicity level that is optimal for any given r, and makes that solution more likely to be stable. In general increasing relatedness increases the range of non-cryptic stable solutions. The higher the relatedness, the closer the individual best strategy is to the group optimum, which tends to be higher toxicity and conspicuousness. The strategy is less liable to cheating (copying appearance with less toxicity), since, if you cheat, you harm your relatives whilst helping yourself.

If we substitute some plausible functional forms for the general functions used in the model, then we gain some further insights. Specifically Appendix 2 demonstrates that high toxicity tends to occur when the population of prey is large, the relatedness in the population is large, detection probability is large (even when maximally cryptic), learning occurs quickly, fecundity declines slowly with toxicity, the probability of attack declines quickly with information of toxicity and the level of toxicity needed to be aversive is large.

Note that when death can only occur through predation (i.e. $\lambda = 0$) and relatedness has no effect ($a = 0$), there is an optimal toxicity independent of appearance. This can be explained by the fact that each individual just finds its best level (any population using some trade-off between toxicity and appearance is invaded by an individual with identical appearance and optimal toxicity). When other mortality factors and/or relatedness feature, then there is an optimal level of toxicity for any appearance.

The present model compared to that of Leimar et al. (1986)

The key difference between the model of Leimar et al. and ours is the assumptions about the predator population. In their model, there are essentially a group of new predators emerging at the start of a season and then continuing to learn over time, so that learning causes changes in the predation pressure over time. This is, in our view, eminently reasonable in a study that aims to

examine the initial origins of aposematism, in which all predators were initially naïve. Here, by contrast, we consider an equilibrium situation, where there is no change in predation pressure over time. The equilibrium level may have been reached by learning, or genetic inheritance or a combination of the two. However the equilibrium is maintained essentially because there is always a balanced mix of young and old individuals in overlapping generations. After the initial evolution of aposematism, the Leimar et al. model might thus correspond ecologically to seasonal predators such as wasps, and ours to more long-lived predators, such as birds and lizards.

Note that in Leimar et al's model solution (2) – where there is non-zero investment in toxins but not sufficient to cause aversion - is not possible as (in their model) all non-zero t are aversive, and learning can never make a predator more likely to eat something, so as time goes on all prey individuals are in less and less danger. Leimar et al's solutions can include a maximally cryptic ESS with either no investment in defences (solution 1) or with defences sufficient to cause aversion (solution 3) with a single ESS $r>0$, as opposed to the range of solutions $r>R$ that we generate.

It should be noted that Leimar's solutions are not true co-evolutionary ESSs, in the sense that they fix one parameter (e.g. t) and then find the optimal solution with the other. If we did this, our model would also yield (at most) one stable solution $r>0$. Conversely if both of their parameters were allowed to vary simultaneously it is possible that solutions similar to ours would be generated. Indeed it seems logical that a range of r values would be stable. The non-cryptic solutions rely on predators recognising the prey and avoiding them. Thus any appearance that is sufficiently visible may suffice, as long as all individuals of the species look the same.

Leimar et al's model always yields at least one point solution (i.e. where all individuals have identical appearance). Ours yields no point solution under some circumstances. In this case the benefits of crypsis are outweighed by the similarity of appearance to other edible forms, and a spread of appearances to dilute the information the predator receives about the attractiveness of this type of prey is optimal.

One of Leimar et al's key predictions was that a non-cryptic ESS could only occur if predators are reluctant to attack prey that are more conspicuous than those so far encountered, or that faster learning occurred with the more conspicuous individuals. This is not necessary in our model, which has ESSs where there is no greater tendency to avoid the more conspicuous individuals, unless there is evidence that they are toxic; indeed the precise mechanisms of learning are not central to our model as they are to Leimar et al's (although they indirectly affect it through the functions $H(t)$ and $L(r)$, as explained above). Leimar concludes that an increased level of survival of attacks with $t>0$ is important to allow ESSs featuring non-zero investment in defence to exist, and we are in full agreement with this conclusion.

Conclusions

There has been recent speculation (Summers & Clough, 2001), that there may be a positive relationship between the conspicuousness of aposematic signals and the strength of the defence that they advertise. Here we present the first explicit mathematical model that can explore this suggestion, and our model predictions support this conjecture.

Our model makes the novel prediction that if conditions support the evolution of a sufficiently strong defence that the prey are aversive and advertise that defence in a conspicuous appearance, then a broad range of alternate ESSs are possible. The specific ESS reached depends on the history of a particular local prey population. Hence, the model suggests that the great diversity of levels of defence and appearance of aposematic prey does not necessarily require special explanation but is an emergent consequence of the co-evolution of defence and signal of that defence.

The theoretical literature in relation to secondary defences is currently unclear about whether or how much we can expect cryptic prey to be defended. Leimar et al. (1986) and also Speed & Ruxton (2004) both suggest that when the threat from predators is small cryptic prey should not invest in secondary defences. However, many other authors assume that cryptic prey can in fact be highly defended (e.g. Harvey et al., 1982; Yachi & Higashi, 1998; Servedio, 2000; Speed, 2001; Brodie & Agrawal, 2001). In this work, we predict that in some cases (with high costs and/ or low predation risk) maximally cryptic prey will be undefended. In other cases such as when there is a

higher risk of predation they will be defended but only moderately: sufficiently to enhance individual survival but not sufficiently to make them aversive to predators. In still other cases prey will be sufficiently defended to be aversive, but still choose not to signal this if the costs of conspicuousness are too great. One important consequence is that aposematic coloration is not necessarily the optimal state for prey that posess substantial defences. Our model also makes the novel prediction of a stable prey strategy that involves very high levels of variability in appearance in prey, combined with moderate and variable levels of defence. At present expectation in many theoretical models is that pro-apostatic selection favours diversity in edible, undefended prey populations but that as soon as there is any level of defence selection becomes anti-apostatic, favouring uniformity (Mallet & Joron, 1999). However we indicate here that one class of stable evolutionary result is a combination of some moderate investment in secondary defence with high levels of diversity in the prey appearance.

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Appendix 1: Derivation of ESS solutions

Let us assume that we have a single species, in which (almost) all individuals possess the parameters t_1, r_1, θ_1. Let us consider a small group with alternative parameters t,r,θ. t_1, r_1, θ_1 is an ESS if and only if the reward to a t_1, r_1, θ_1.-individual in such a population is greater than the reward to a t,r,θ-individual, for any possible set of alternative parameters t,r,θ. We shall consider local ESSs only, where it is assumed that alternative strategies are mutations which are very close to the original values.

Relative payoffs

We represent the average relatedness of individuals in the "local" area by *a*. We assume that the population in this area consists of a proportion of identical individuals *a* which plays the alternative strategy *t,r,θ,* the remaining members of the population being unrelated to this group and playing t_1, r_1, θ_1. The payoff to an individual playing a mutant strategy is given by

$$P(t, r, \theta; t_1, r_1, \theta_1) = \frac{F(t)}{\lambda + D(r)K(t)Q(I)} \qquad (12)$$

where

$$I = \frac{N}{n}\{aL(r)H(t)S(r, r, \theta, \theta) + (1-a)L(r_1)H(t_1)S(r, r_1, \theta, \theta_1)\},$$

$$S(r, r_1, \theta, \theta_1) = S(\sqrt{r_1^2 + r^2 - 2r_1 r\cos(\theta_1 - \theta)})$$

and $S(0)=1$.

The payoff to a resident (averaged over a much larger area) is

$$P(t_1, r_1, \theta_1; t_1, r_1, \theta_1) = \frac{F(t_1)}{\lambda + D(r_1)K(t_1)Q(I_1)}$$

where

$$I_1 = \frac{N}{n}L(r_1)H(t_1)$$

I is the toxicity information for the mutant in the local area, and I_1 is the toxicity information for the resident over the larger area (essentially unaffected by the mutant). To obtain the inclusive fitness for both mutant and resident the payoffs should be multiplied by the term *(1+a(N-1))*; we leave this term out as it has no effect on our results.

Optimal toxicity

The ESS value of *t* can be found by solving the following equation at $t = t_1, r = r_1, \theta = \theta_1$.

$$\frac{\partial}{\partial t} P(t, r, \theta; t_1, r_1, \theta_1) = 0 \Rightarrow$$

$$g_1(r_1, t_1) = \left(\frac{\lambda + D(r_1)K(t_1)Q(I_1)}{D(r_1)K(t_1)Q(I_1)} \frac{F'(t_1)}{F(t_1)} - \frac{K'(t_1)}{K(t_1)} - aI_1 \frac{Q'(I_1)}{Q(I_1)} \frac{H'(t_1)}{H(t_1)} \right) = 0 \qquad (13a)$$

Note that it is also possible for $t_1 = 0$ to be stable, which occurs if

$$g_1(r_1, 0) < 0 \qquad (13b)$$

For the sake of simplicity we shall assume that there is precisely one value of t_1 which satisfies these conditions (a reasonable assumption for well behaved functional forms). If there is only one such solution, then if this solution involves $t_1 > 0$ the solution must be stable. If this were not so, the fitness function for *t* just above t_1 will be higher than that for t_1, but as the fitness must eventually decline for very high t, there will be a higher root of (13a). In fact we show below that whenever $I_1 > 0$ ($t > t_c$), the (unique) optimal value of *t* increases as *r* increases, so if optimal toxicity is aversive for any value of r_1, it is for all larger values of *r*, under reasonable assumptions.

$g_1(r_1, t_1)$ is increasing with r_1 provided that $I_1 > 0$, $V(i) = -iQ'(i)/Q(i)$ is increasing with positive i at the critical value r_1 and $D(r_1)Q(I_1)$ increases with r_1.

Increasing conspicuousness (r_I) will certainly increase the rate at which prey are detected by predators (D). However, increasing r_I will increase I_I which in turn will decrease the probability that that detection leads to attack (Q). So the rate of attack (the product DQ) could in principle increase, decrease, or in the limiting case stay the same as conspicuousness (r_I) increases. Indeed it would be possible to pick functional forms to achieve all these possible effects. However we consider that for the overwhelming majority of biologically plausible formulations D will increase faster with r_I than Q decreases, and so the production DQ will increase with increasing r_I. Our arguments are as follows. As the prey becomes more conspicuous (r_I increases) then the range of distances over which it can be detected will increase. Since almost all prey live in habitats where predator-prey interactions occur in two or three dimensions, a small increase in detection distance can lead to a large increase in encounter rate (D), because of the geometric effect. Although increasing conspicuousness will reduce the likelihood of an encounter leading to an attack, this probability will not be affected by geometry in the same way, so we would not expect this probability (Q) to decrease quickly enough with increasing r to compensate for the dramatic increase in D with increasing conspicuousness. Further, we would expect Q to be a more or less rapidly saturating function of conspicuousness r_I so that its influence over prey protection is generally much more limited than the effects of r_I on detection rates. In models of classical conditioning, for example, avoidance learning rates are often described as the product of conspicuousness and unpalatability, suggesting rapid saturation, esp. when prey are not very highly defended (see e.g. Servedio 2000; Speed 2001). Furthermore an additional mechanism that causes the predator to attack conspicuous defended prey is confusing them with other prey types that are defended and cryptic, once conspicuous has increased sufficiently that such confusion is unlikely, further increases in conspicuousness will have little effect on Q. In contrast, there is less reason to expect a similar saturating effect whereby increasing conspicuousness does not lead to increased encounter rates except for large values of r (remembering that we only assume DQ to be increasing at r_I) without imposing special assumptions of the habitat structure of animal movement, so again, from this reason our expectation is that the product DQ will increase with increasing conspicuousness (increasing r_I).

It should be noted here that these conditions are sufficient, but not necessary, so for instance if *V(i)* is increasing rapidly, then $D(r_1)Q(I_1)$ could be decreasing (as long as this is not too quickly) with the same result. In fact there is a link between these two assumptions. If *L(r)=K D(r)* for some constant K (reasonable given the relationship between these two functions) then $D(r_1)Q(I_1)$ increasing is the same result as $V(I_1)<1$. We shall assume that these results are true. Similarly at $g_1(r_1,t_1)=0$, the function decreases with *t* under our assumption of a unique solution, since there is either a unique solution with $t_1=0$ and $g_1(r_1,0)<0$ or $g_1(r_1,0)>0$ and there is a unique solution with $g_1(r_1,t_1)=0$.

Thus there is a unique solution for t_1 for every r_1, which is increasing with r_1.

So any solution must include this optimal level of toxicity. We next proceed to find the values of r_1 and θ_1 which can be stable in conjunction with this. Note that in the special case where $\lambda=a=0$, the optimal level of toxicity is independent of appearance (but not of aversiveness, as it affects this through *H(t)*). It may seem strange that optimal toxicity can be independent of appearance. However, natural selection acts at the level of the individual, and a stable solution is one that cannot be beaten by an invader. Any situation where the population does not choose the level of toxicity dictated by the trade-off between *F* and *K*, e.g. to be more toxic to deter predation, will be invaded by individuals which have the same appearance but choose the trade-off level. In the case where λ is non-zero (but *a=0*), there is a link between optimal *t* and appearance, for the sole reason that appearance affects the relative contribution of predation and other factors to mortality (given by $D(r_1)Q(I_1)K(t_1)/\lambda$). There is thus a unique value of t_1 which is the optimal toxicity level for any given r_1. We have to find which value(s) of r_1, if any, give ESSs.

The maximum crypsis solution (r_1=0)

Firstly we look at the possibility of a solution with $r_1=0$ (note that this automatically means that the value of θ_1 is irrelevant). We only need to consider invasion by larger values of *r,* i.e. show that

$$\frac{\partial}{\partial r} P(t_1, r, \theta_1; t_1, 0, \theta_1) < 0$$

$$g_2(0, t_1) + g_3(0, t_1) > 0$$

yielding

$$\frac{D'(0)}{D(0)} + I_1 \frac{Q'(I_1)}{Q(I_1)} \left(S'(0)(1-a) + a \frac{L'(0)}{L(0)} \right) > 0 \qquad (14)$$

The second term is positive for some functions *L(r)* and *S(y)* (and for sufficiently small *a*) if and only if $H(t_1) > 0$. In this case $r_1 = 0$ is clearly stable.

This means that for some functional forms being completely cryptic is always an ESS providing the best value of *t* is sufficiently toxic to be aversive, in the sense of reducing attacks by predators.

Other point solutions ($r_1 > 0$)

If $r_1 > 0$ then the value of θ_1 is relevant, and we have to consider invasion by both larger and smaller values of *r* and different values of θ. Considering $\theta = \theta_1$ initially, we are interested in the derivative

$$\frac{\partial}{\partial r} P(t_1, r, \theta_1; t_1, r_1, \theta_1)$$

which is discontinuous at $r = r_1$ due to the similarity function *S*. The derivative becomes

$$\frac{\partial}{\partial r} P(t_1, r, \theta_1; t_1, r_1, \theta_1) = -g_2(r_1, t_1) - g_3(r_1, t_1) \frac{\partial}{\partial r} (| r - r_1 |)$$

For a stable solution we need this derivative to be positive for $r < r_1$ and negative for $r > r_1$. This is equivalent to

$$g_2(r_1, t_1) - g_3(r_1, t_1) < 0 \qquad (15a)$$

$$g_2(r_1, t_1) + g_3(r_1, t_1) > 0 \qquad (15b)$$

Note that the discontinuity in the derivative at r_1 means that there is not a unique equilibrium value and the conspicuousness level r_1 is stable provided that (15) is satisfied. Equation (15a) is more difficult to satisfy than (15b) (unless *a* is unrealistically large). It is easy to see that it is impossible to satisfy this for $H(t_1)<0$ ($I_1<0$). If $H(t_1)>0$ then we require

$$\frac{D'(r_1)}{D(r_1)} - I_1 \frac{Q'(I_1)}{Q(I_1)}\left(S'(0)(1-a) - a\frac{L'(r_1)}{L(r_1)}) \right) < 0 \qquad (16)$$

Allowing $\theta \neq \theta_1$ does not impose any further restrictions (invasion by such a strategy is easier to resist whenever $H(t_1)>0$). Any solution satisfying conditions (13) and (16) is thus stable.

On the (reasonable) assumption that $D'(r)/D(r)$ is decreasing, then if either $L(r)=K\,D(r)$ for some constant *K* or *a* is small, t_1, r_1, θ_1 is a local ESS if $R < r_1 < \infty$ for some critical value *R* (in addition to the possible crypsis $r_1 = 0$ solution). This is a sufficient condition only; this result may occur even if the above is not satisfied. (Similarly, the result may hold even if $D(r_1)Q(I_1)$ does not increase with r_1, and because of the discontinuity in the derivative of the fitness function with respect to *r*, the local ESSs are likely to occur for values of r_1 lying in an interval). This value of *R* may be infinite, which would mean that no solution with $r_1 > 0$ exists.

To see this, consider the following. The criterion (16) reduces to

$$V(I_1) > -\frac{D'(r_1)}{D(r_1)} \Bigg/ \left(S'(0)(1-a) - a\frac{L'(r_1)}{L(r_1)} \right)$$

where the right-hand side of the above is positive. Given that optimal t_1 does not decrease with r_1, then I_1 increases with it so that the left-hand side of the above increases whilst the right-hand side decreases. Thus the critical value *R* is given by

$$V(I_1) = -\frac{D'(R)}{D(R)} \Big/ \left(S'(0)(1-a) - a\frac{L'(R)}{L(R)} \right) \qquad (17)$$

Solution summary

t=0 and *r*=0 when $g_1(0,0) < 0$, $g_2(0,0) + g_3(0,0) > 0$

t>0 and *r*=0 when $g_1(0,t_1) = 0$, $g_2(0,t_1) + g_3(0,t_1) > 0$

t=0 and *r*>0 can never occur

t>0 and *r*>0 when $g_1(r_1,t_1) = 0$ ($t_1 > t_c$ also needed),

$g_2(r_1,t_1) - g_3(r_1,t_1) < 0$

A unique ESS, multiple ESSs or no ESSs?

We have an infinite set of candidate solutions given by the pair *(r,t(r))*, for all positive *r*, where *t(r)* is obtained from condition (13) and is non-decreasing with *r*, as soon as *t(r)* reaches t_c (recall that t_c is the value for which H(t_c)= I_1=0).

If t(r)< t_c for all values of *r*, then we know that all of these solutions are unstable, except possibly when *r=0*. This occurs if the optimal value of *t* in the limit as *r* tends to infinity is not greater than t_c, i.e.

$g_1(\infty,t_c) < 0$

so that

$$\frac{\lambda + D(\infty)K(t_c)Q(0)}{D(\infty)K(t_c)Q(0)}\frac{F'(t_c)}{F(t_c)} - \frac{K'(t_c)}{K(t_c)} < a\frac{N}{n}L(\infty)H'(t_c)\frac{Q'(0)}{Q(0)} \qquad (18)$$

if (18) is true then t(0)< t_c and so for r_1=0 we have I_1<0. Thus there is a unique ESS at r_1=0 if (14) and (18) hold, otherwise no ESSs if (18) but not (14) holds.

If (18) does not hold, there will be multiple solutions with r_1>0, as well as a solution with r_1=0 if and only if (14) holds.

Non-point solutions

It is possible to have a solution where not all of the population look alike. In particular there are sets of functions where no point solution is possible. Since, for sufficiently small *a*, r_1=*0* is always a solution when *H(* t_1 *)>0* we shall briefly consider the situation where *H(* t_1 *)<0.* In this case each individual gives information of the non-toxicity of those that it resembles, so that it is best to look as little like the other species members as possible. For any given value of r_1, it is clear that the best distribution over θ is a uniform one on (0,2π).

If a population follows this distribution of θ, then

$$I_1 = \frac{N}{n}L(r_1)H(t_1)\int_0^{2\pi}\frac{1}{2\pi}S((2r_1^2 - 2r_1^2\cos(\theta))^{0.5})d\theta = \frac{N}{n}L(r_1)H(t_1)\int_0^{\pi}\frac{1}{\pi}S(2r_1\sin\psi)d\psi$$

In fact such a solution is unlikely to be stable, since it would be invaded by a small group that chooses a smaller *r*, and gets further in appearance from the others and reduces conspicuousness. A solution is likely to cover a range of values of r_1. Calculation and checking for stability in this case will be difficult for real functions, and will probably require numerical solutions. Any solution will be in the form of a density function
P(r,θ)=C(r)/2πr , i.e. dependent on r but not θ.

It will satisfy the following two conditions:

(i) the payoff to all individuals in the population must be identical

(ii) C(r) is continuous and there will be a unique point, r(r_m), where C(r_m)=0 (otherwise individuals could change to marginally larger r with greater payoff), giving

$$N = \int_0^{rm} C(r)dr$$

Assuming that a=0, we expect a solution will be of the form

1) $D(w)Q(I(w))=D(0)Q(I(0))$ for all w.

2) C(r_m)=0

$$3)\ I(w) = H(t)\int_0^{rm} L(r)C(r)\int_0^{2\pi}\frac{1}{2\pi}S((w^2 + r^2 - 2wr\cos(\theta))^{0.5})d\theta dr$$

so that

$$I(0) = H(t)\int_0^{rm} L(r)C(r)\int_0^{2\pi}\frac{1}{2\pi}S(r)d\theta dr = H(t)\int_0^{rm} L(r)C(r)S(r)dr$$

We conjecture that there will usually be a unique solution of this type.

Appendix 2: Example functions

We now consider some examples of the functions described above to show the type of solutions which can occur.

$$F(t) = e^{-t/\alpha}, K(t) = \frac{k}{1+t/\beta}, H(t) = t - \gamma$$

$$D(r) = L(r) = \frac{d_0}{d_0 + (1-d_0)e^{-r}}$$

$$S(y) = \max(1 - \nu y - \nu_2 y^2, 0).$$

Finally the information function *Q* is given by

$$Q(x) = \begin{cases} q_0 e^{-x\kappa}, & x > 0 \\ 1 - (1-q_0)e^{\frac{xkq_0}{1-q_0}}, & x < 0 \end{cases}$$

This yields a unique value for optimal *t,* given by

$$g_1(r_1, t_1) = -\frac{\lambda(\beta + t_1)e^{\kappa(t1-\gamma)D(r1)N/n} + D(r_1)\beta kq_0}{D(r_1)\beta kq_0}\frac{1}{\alpha} + \frac{1}{\beta + t_1} + a\frac{N}{n}\kappa D(r_1)$$

This general expression works only for $t > t_c$ (the ratio of the derivative of Q and Q is a little more complex for $t < t_c$, but the principle is no different). All solutions when $t < t_c$ are unstable unless *r=0*, as mentioned earlier.

In the simplifying case where $\lambda = a = 0$, we obtain

$t_1 = Max(\alpha - \beta, 0)$, independently of *r*, which works whether $t_1 > t_c$ or not.

$r_1 = 0$ is an ESS if

$$\frac{D'(0)}{D(0)} + I_1 \frac{Q'(I_1)}{Q(I_1)} \left(S'(0)(1-a) + a\frac{L'(0)}{L(0)} \right) > 0$$

When *a=0* we obtain

$$I_1 S'(0) \frac{Q'(I_1)D(0)}{Q(I_1)D'(0)} > -1 \Rightarrow I_1 > -\frac{(1-(1-q_0)e^{\kappa I 1 q 0/(1-q0)})d_0(1-d_0)}{-\nu \times -q_0 \kappa e^{\kappa I 1 q 0/(1-q0)} d_0} = -\frac{(1-d_0)}{\kappa \nu q_0}(e^{-I 1 \kappa q 0/(1-q0)} - (1-q_0))$$

for negative I_1 (it is trivially true for positive I_1). This is clearly satisfied when I_1 is near 0 and when it is very large and negative, but possibly can be violated for intermediate values. Thus instability occurs in a critical range of information I_1 only, which for some parameters may be empty; if I_1 is large and negative then individuals are very attractive to predators and maximum camouflage is best, if I_1 is near zero individuals are slightly attractive to predators but cannot improve things much by changing appearance, so staying at *r=0* is again best. For intermediate values individuals may be able to reduce their attractiveness by moving away from their current appearance, even though they will be discovered by predators more often. r_1 *=0* is more likely to be a solution if the rate of decline of attacks as toxicity increases declines slowly, predators cannot identify differences between individuals for discriminatory purposes very well or camouflage is very effective. As long as *a* is not very large, the same pattern occurs for non-zero *a*.
r_1 *>0* is an ESS if

$$\frac{D'(r_1)}{D(r_1)} - I_1 \frac{Q'(I_1)}{Q(I_1)} \left(S'(0)(1-a) - a\frac{L'(r_1)}{L(r_1)} \right) < 0$$

This is only possible if I_1 *>0.* For *a=0* we obtain

$$I_1 S'(0) \frac{Q'(I_1)D(r_1)}{Q(I_1)D'(r_1)} > 1 \Rightarrow I_1 > \frac{(1-d_0)e^{-r1}}{\kappa \nu (d_0 + (1-d_0)e^{-r1})}$$

If further λ=0 then

$$I_1 = \frac{N}{n}\frac{d_0}{d_0 + (1-d_0)e^{-r}}(\alpha - \beta - \gamma)$$

which yields

$$\frac{Nd_0\nu\kappa(\alpha - \beta - \gamma)}{n(1-d_0)} > e^{-r1} \Rightarrow r_1 > R = \ln\left(\frac{n(1-d_0)}{\kappa d_0 N\nu(\alpha - \beta - \gamma)}\right)$$

so that any value of r_1 that is sufficiently large will be stable (and for some parameter values this will be true for all *r*, since R will be negative). Hence, beyond some threshold value of conspicuousness, any common form will be stable.