ORIGINAL ARTICLE

THE IMPORTANCE OF INITIAL PROTECTION OF CONSPICUOUS MUTANTS FOR THE COEVOLUTION OF DEFENSE AND APOSEMATIC SIGNALING OF THE DEFENSE: A MODELING STUDY

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Most models of the evolution of aposematic signaling assume (1) that the secondary defense being signaled is fixed, and (2) that conspicuous mutants arising in a population of defended individuals of cryptic appearance are initially protected from predation. Previous models of ours relaxed the first assumption, here we relax the second and compare with our earlier work to explore the consequences of initial protection from predation on the coevolution of secondary defense and aposematic signaling. As expected, we find that aposematic signaling evolves more easily if initial protection is available. Less obviously, the coevolved level of secondary defense should also be higher if initial protection is provided. Across species or populations, we predict that when initial protection occurs, then strength of aposematic signal should be correlated with the strength of the underlying secondary defense, whereas no such correlation should occur without initial protection. Finally, we demonstrate that species can invest heavily in a secondary defense and remain maximally cryptic (forgoing the advantages of aposematic signaling) and that within a species we should expect strong variation in appearance between populations but much less variation within populations. Hence, we demonstrate that whether conspicuous morphs receive initial protection from predation has powerful and potentially empirically detectible consequences for the coevolution of secondary defenses and aposematic signaling.

KEY WORDS: Aposematism, camouflage, coloration, evolutionarily stable model, insects, secondary defenses, toxicity, warning signals.

Introduction

Many potential prey species have a toxic or other secondary defense against predators, and in some cases advertise this defense with conspicuous coloration (a classic example being the yellow and black stripes characteristic of wasps; Cott 1940; Edmunds 1974). These so-called aposematic signals can be effective if the prey is sufficiently well defended that at least some predators would benefit from forgoing the chance to attack or from

attacking more circumspectly (Guilford 1992. It is generally considered that the signal acts to aid the predator in generalizing from previous aversive experience with similar looking individuals and learning to recognize and avoid similar looking prey in future (Wallace 1867; Ruxton 2004). It is well known that the initial evolution of aposematism produces greater challenges than its subsequent maintenance because the advantages of warning displays are positively density dependent (Muller 1879; Mallet 1987; Ruxton 2004). That is, aposematic individuals benefit if they are common in the environment because then the costs of educating initially naive predators are shared over more individuals. Hence, various mechanisms have been suggested for how the mutant aposematic morph can grow in number, at least locally, before they feel the full pressure of predation.

Suggestions range from stochastic effects of random drift in populations (Mallet and Singer 1987) to heightened and prolonged avoidance of novelty in prey populations (Marples et al. 1998b, 2005; Marples and Kelly 1999; Kelly and Marples 2004), and even to effects of maternal inheritance on expression of aposematic displays (Brodie and Agrawal 2001). Furthermore, recent theoretical and empirical work suggests that conspicuousness itself may evolve easily in unprofitable species because raised apparency to predators is generally too expensive for edible prey to maintain (Sherratt 2002; Sherratt and Beatty 2003; Sherratt and Franks 2005).

One notable thing about most such explanations of the evolution of aposematism is an assumption that only the warning display itself evolves, whereas the secondary defense—the toxin, sting, or spines that are being advertised—are fixed, invariant properties of the prey in question (Mallet and Singer 1987; Ruxton et al. 2004). However, some recent models have begun to take seriously the challenging suggestion of Leimar et al. (1986) that aposematic traits may coevolve with the secondary defenses that they advertise.

Leimar et al. (1986) proposed, for example, that aposematic display may evolve antagonistically with respect to secondary defense, so that as bright warning displays evolve, investment in costly toxins may decline. Speed and Ruxton (2005) demonstrated the plausibility of this suggestion in a stochastic individual-based model. While individual-based modeling has the strength of considerable utility and flexibility, it does not necessarily define the causal basis of characteristic emergent properties, nor does it describe parameter boundaries for specified aposematic conditions. In contrast, Broom et al. (2006) developed an analytical evolutionarily stable strategy (ESS) model inspired by, but more general than, the one proposed by Leimar et al. (1986). Whereas Leimar et al. described the properties of a single predator in detail and applied this to a prey population. The model of Broom et al. considered the effects on prey of a set of "equilibrium predators," assuming that naive individuals entered the population at the same rate as experienced individuals left.

In the present article, we have adopted this approach because the specific learning rules used by predators in realistic circumstances are poorly understood and likely to be highly variable (see the discussion in Lynn 2005), and the predictions of previous models of evolution of aposematism have been demonstrated to be relatively sensitive to this fine detail (Servedio 2000; Speed 2001). Further, although highly seasonal predator populations with low individual mobility may be well characterized by a cohort of predators, each at a similar stage of learning, for longer-lived and highly mobile predators (such as the birds often considered in studies of aposematism) we feel that the suite of predators to which an individual prey item is exposed will often comprise individuals at different stages of learning.

Our original model assumed an initial numerical advantage to mutants, effectively by assuming that mutants existed as a non-negligible proportion of the population within a local area (presumably by one of the mechanisms discussed previously), and made predictions about the coevolution of secondary defense and appearance.

However, it is at least equally valid to ask how defensive traits may coevolve if we relax this assumption, and look at the situation in which mutants experience predation at all times and do not get the cushion of early protection from predators. In this article we explore how the absence of a period of early protection would affect the coevolution of defense and appearance. Our expectation is that this should make evolution of conspicuous aposematic signals more difficult, whereas the effect on the evolution of defense is less clear. Furthermore, comparison of our original model (with the cushion of early protection) and our modified version described here (without this early protection for new aposematic mutants) should help us to understand the importance of variation in evolutionary histories of aposematic traits across prey species.

We first describe the original model and, after describing modifications, consider the importance of starting points on the subsequent optimization of aposematic traits.

The Original Model of Broom et al. (2006, 2007)

We have an effectively infinite population of prey individuals, each described by a phenotype of the form (t, r, θ). The letter t indicated the toxicity of the individual, with increasing values indicating increasing toxicity and $t = 0$ being the minimal level of toxicity; r is the conspicuousness of the individual, with increasing values indicating increasing conspicuousness, a maximally cryptic individual has $r = 0$. The appearance of the individual is described by polar coordinates (r, θ) with $\theta \in [0, 2\pi)$ describing

aspects of appearance that do not influence conspicuousness. So two individuals that have the same r, but different θ would be equally as conspicuous to predators but would look identifiably different from each other.

There are costs and benefits to a toxic secondary defense. The assumed cost is that the fecundity of the individual F is a declining function of t:

$$F(t) = f_o \exp(-ft) \qquad (1)$$

for positive constants f_o and f. This can be interpreted as toxic defenses requiring metabolic energy for their generation and/or maintenance that must be diverted from investment in reproduction. In fact in the original model of Broom et al. (2006), the analysis was carried out with a more general fecundity function $F(t)$. This is also true of the other functional forms that follow. The analysis was then developed further in Broom et al. (2007) with plausible example functions that made the results easier to interpret while maintaining much of the generality, and these are the functional forms used in this article. Although we provide the model in full here, together with brief biological interpretation, we refer interested readers to the earlier publications for a full justification of each model assumption.

There is a direct benefit to toxicity, such that the probability (K) of being killed in an attack by a predator declines with increasing toxicity:

$$K(t) = \frac{k_o}{1 + kt} \qquad (2)$$

for positive constants k_o and k.

There is also an indirect benefit in that predators that attack highly toxic prey find the experience aversive and become less likely to attack similar looking prey in future. We model this as follows. First we define the aversiveness (H) of a prey individual as

$$H(t) = t - t_c \qquad (3)$$

for some positive constant t_c.

Thus, the predator finds attacking prey with toxicities higher than t_c to be aversive experiences, whereas those with toxicities lower than t_c are considered to be positive experiences. Hence in cases of toxicities lower than t_c, but greater than zero, prey could contain small quantities of toxins, but the cost to the predator of ingesting these is outweighed by the nutritional benefits of consuming the prey. We class such prey as possessing some defense that is not sufficient to be aversive.

We do not define the rate (D) at which a prey item is detected by predators explicitly. We did use an example function in Broom et al. (2006), but dropped this for a more general form in Broom et al. (2007). We assume that any plausible functional form has the following three properties: (1) D increases with increasing r (but this rate of increase does not increase with r); (2) $D(0) > 0$, so that even maximally cryptic prey have some chance of being detected; (3) there is a maximum possible value of $D(r)$, d_m, so that the encounter rate does not increase unboundedly with the brightness of coloration.

When an individual is detected, there is a probability Q that it will be attacked:

$$Q = \min(1, q_o \exp(-qI)) \qquad (4)$$

where q_o and q are positive constants and I is the information that the predator has about individuals that look similar to the focal individual.

For a population with N prey items, and n predators, and for prey individual i, the information about the toxicity of this individual is given by

$$I_i = \frac{1}{n} \sum_{j \neq i}^{N} D(r_j) H(t_j) S_{ij} \qquad (5)$$

where S_{ij} is the visual similarity between individuals i and j, and individual j has the parameter values (t_j, r_j, θ_j) for all j. We shall assume that both predator and prey populations are large, and define $P = N/n$. When a particular predator encounters individual i, the information that it has about that individual is drawn from memories of previous encounters with other individuals. $D(r_i)$ influences the likelihood that a particular individual j has already been encountered by this predator, H describes the predator's recollection of that encounter (either as an aversive or positive experience), and S describes the influence of that encounter with j on the current encounter with i, such that the more influential j is, the more similar the two individuals appear. Specifically, we define S as a declining function of the Euclidian distance (x_{ij}) between the two individuals in (r, θ) space:

$$S_{ij} = S(x_{ij}) = \max(1 - vx_{ij}, 0) \qquad (6)$$

for some positive constant v. D and therefore I will increase with conspicuousness, and thus predators will tend to have greater knowledge of more conspicuous prey types. This mirrors the traditional view that conspicuousness enhances the speed of aversion learning (Gittleman et al. 1980). Our results would hold for any generalization function S_{ij} that has a similar peaked shape, in which small deviations from similarity do not have a negligible effect; a similar (but biologically plausible) restriction on the shape of generalization functions has been shown in other models in the context of the evolution of mimicry (see discussion in Balogh and Leimar 2005). However, it is important to bear in mind that our results would not hold if the maximum of the generalization curve were smooth (like a normal curve) rather than peaked. For a given peaked generalization curve our results are robust for any logical measure of the distance between two individuals (x_{ij}).

The reproductive payoff (Z_i) to individual i is given by the rate at which that individual can produce offspring F, multiplied by the expected lifetime of the organism before being killed by a predator. Thus,

$$Z_i = \frac{F\,(t_i)}{D\,(r_i)\,Q\,(I_i)\,K\,(t_i)} \qquad (7)$$

Finding Evolutionarily Stable Strategies

These are found simply by comparing the payoff to an individual from a resident population that has phenotype (t_1, r_1, θ_1) with that of a mutant that has phenotype (t, r, θ). In the original model the subpopulation of mutants was allowed to grow to a finite size before it felt the pressure from predation. Specifically, it was assumed that although the mutants made up a negligible part of the whole prey population, they were numerous locally, so that any predator that encounters a mutant would have previously encountered mutants on a fraction a of its previous encounters, the residue of encounters being with resident types. Thus, for the whole population, the information relating to the resident phenotype was simply that of a monomorphic population:

$$I_1 = P D\,(r_1)\,H\,(t_1) \qquad (8)$$

whereas for the mutants, it was

$$I = P(aD\,(r)\,H\,(t) + (1-a)D(r_1)H(t_1)S(r,\theta,r_1,\theta_1)) \quad (9)$$

where $S(r,\theta,r_1,\theta_1)$ is the value of the similarity function between a mutant and a resident individual.

Thus, the parameter a describes the initial protection that the mutant gains from predation that allows it to flourish locally before predation pressure is felt. Here we look at the limiting case in which this protection is denied (i.e., the limit $a \to 0$) and compare it with the results of Broom et al. (2007).

Note that implicit in our formulation is that the fitness of an individual is a function only of its own lifetime reproduction. Thus, we do not consider kin-selected benefits that may accrue because the death of an individual may reduce the predation pressure on nearby kin through aversion learning by the predator. While this effect is possible, on empirical grounds, we expect the benefits to accrue on the basis of similarity of appearance rather than kinship. Further, the extent to which prey individuals that share the same potential predator (i.e., that are spatially close) are genetically related will likely be highly variable between (and indeed within) systems. Thus, a should best be interpreted as a measure of local density of the phenotype at the time when predation first occurs. However, the most likely reason that a proportion of locally existing individuals have the same mutant phenotype is that they are closely related. Thus, kin structuring is likely to be an important prerequisite of a mutant phenotype rising to a nontrivial local density.

Results

LEVEL OF TOXIC DEFENSE

In the original model of Broom et al. (2006), the equilibrium values of toxicity and conspicuousness were shown to be linked according to

$$t\,(r) = \frac{1}{f - aq P D\,(r)} - \frac{1}{k} \qquad (10)$$

If this calculated value is negative, then $t = 0$ is the equilibrium value.

Taking the limit, $a \to 0$, this simplifies considerably to

$$t = \frac{1}{f} - \frac{1}{k} \equiv t_o \qquad (11)$$

where t_o is the unique equilibrium value of t, independent of r. We can make several observations from this. First, when the prey receives initial protection from predation then investment in secondary defense is linked to conspicuousness, such that increased investment in this defense is associated with increased conspicuousness; when no initial protection is available, then we expect investment in a secondary defense to be unrelated to conspicuousness. Further, all other things being equal, we expect equilibrium levels of toxicity to be higher for the prey given initial protection than those without. This occurs because with initial protection there are two paybacks for investment in defense, with avoidance learning reducing the likelihood of being attacked as well as the direct benefit of an increased probability of surviving an attack. Finally, we see that in our new model the equilibrium level of toxicity is determined by only two parameters, f and k. The parameter f describes the cost of defense, with increasing f indicating increasing costs of defense. Thus, it is no surprise that increasing f decreases the equilibrium investment in toxic defenses. The parameter k reflects the probability of surviving an attack (for given investment in defense), with increasing k making a given level of defense more likely to lead to the survival of any given attack (and increasing the incremental advantage of increasing defense for lower levels of defense). Thus, increasing k makes investment in a secondary defense more attractive. We note that population sizes or any aspects related to predator avoidance on the basis of appearance have no effect on investment in toxic defenses (unlike the case in our previous model in which initial protection is available). This makes sense because a mutant can only flourish if it can outcompete the resident in the absence of any (frequency-dependent) benefits from predator avoidance learning in the new

model, but not in the original model with initial protection from predators.

CONSPICUOUS APPEARANCE

Conspicuous appearance will only be an equilibrium solution if such appearance aids aversive learning by predators. Thus, sufficient investment in toxicity to make the prey aversive ($t > t_c$) is a necessary requirement for the prey to give up maximum crypsis for antipredatory reasons. However, Broom et al. 2007 demonstrated that it was not a sufficient condition, and that it was possible to get prey that were so toxic as to be aversive but still maximally cryptic. Specifically, the condition for an equilibrium with $r > 0$ was

$$1 - qP(t - t_c) D(r) \left(a + (1 - a) v \left(\frac{D(r)}{D^/(r)} \right) \right) < 0 \quad (12)$$

Now, because t increases with r in the original model (and in our limiting case does not decrease), if equation (12) is satisfied for some $r = R$ then it will be satisfied for any $r > R$. Hence, to demonstrate that no conspicuous solutions ($r > 0$) exist for a given set of parameter values, we need to only demonstrate that equation (12) is not satisfied as $r \to \infty$. We expect that the rate at which predators find prey will saturate with increasing conspicuousness (e.g., due to time spent traveling between prey or handling captured prey). Assuming that the maximum value of $D(r)$ is d_m, then, from equation (10), conspicuous solutions are found providing

$$aqPd_m > \left(f - \frac{k}{1 + kt_c} \right) \quad (13)$$

In our limit where $a \to 0$, this simplifies to

$$0 > \left(f - \frac{k}{1 + kt_c} \right) \quad (14)$$

and hence to

$$t_c < t_o \quad (15)$$

Again some general conclusions can be drawn. Comparison of equations (13) and (14) indicates that conspicuous appearance (and so aposematic signaling) is less likely to evolve when an invading morph does not receive initial protection from predation (exactly as expected from arguments in the Introduction). However, we can also see that the advantage of initial protection increases with the values of a, q, P, and d_m, but none of these factors affect the attractiveness of aposematic signaling in the absence of initial protection. The parameter a describes the extent of initial protection, so its role in equation (13) and absence from equation (14) is no surprise.

Increasing q increases the effectiveness of avoidance learning, and clearly the more effective avoidance learning is the more attractive the aposematic signaling should be. However, in the absence of initial protection, a mutant will only flourish if it can do so without benefiting from avoidance learning, and so the value of q is irrelevant. High prey population size per predator (P), or high encounter rate between predators and prey (high d_m) both aid avoidance learning and so should encourage aposematism in the original model but not in the simplified case where $a \to 0$. Finally, only three parameters affect the existence of conspicuous signals in the absence of initial protection. If the equilibrium value of t is greater than t_c (i.e., prey invest in enough toxins to be aversive), then a conspicuous equilibrium exists.

CRYPSIS

In the original model, the condition for a maximally cryptic solution was

$$1 + qP(t - t_c) D(0) \left((1 - a) v \left(\frac{D(0)}{D^/(0)} \right) - a \right) > 0 \quad (16)$$

In our limit of $a \to 0$, this condition becomes

$$1 + qvP(t_o - t_c) \frac{(D(0))^2}{D^/(0)} > 0 \quad (17)$$

Because we assumed that $D(0) > 0$ and D is an increasing function of r (i.e., $D^/(r) > 0$), then equation (17) is satisfied providing $t_o > t_c$, but it can also be satisfied for specific ranges of parameter values if $t_o < t_c$. Thus, prey may become sufficiently toxic to be aversive, without this necessarily triggering a change in appearance from crypsis to a conspicuous signal. The original model made this same prediction.

From equation (16), we can see that the effect of initial protection on the likelihood of a maximally cryptic equilibrium depends on the parameter group

$$\phi = \frac{vD(0)}{D^/(0)} \quad (18)$$

From equation (16), increasing the initial protection (increasing a) makes this type of equilibrium (in which the prey are aversive but maximally cryptic) less likely, because it makes it easier for an aversive noncryptic prey to acquire the critical mass to deter predators by using aposematic signals.

For nonaversive prey, the higher v is, the more rapidly protection from predator avoidance is lost with any deviation in appearance from the resident form. The higher the $D(0)$ the greater the effect of this loss of protection is, because this is the rate of attack for individuals at maximum crypsis. The higher the $D^/(0)$, the faster the encounter rate with predators increases with deviation from crypsis. This higher encounter rate will facilitate more

effective avoidance learning, especially if v is low, because low v encourages generalization between prey of quite different appearance, and so a mutant would still gain protection through avoidance learning even if it looked a little different from the resident morph. If $D(0)$ is low, then maximally cryptic prey will be encountered less often (per capita) than mutants, so the mutants will contribute disproportionately to the information function. Thus, a low value of ø will encourage the invasion of the maximally cryptic morph by a conspicuous mutant, provided that a is not very large. Even when $a \rightarrow 0$, this equilibrium (in which the prey are not aversive but maximally cryptic) is more likely when q, v, P, and $D(0)$ are small and $D^/(0)$ is large.

COEXISTANCE OF EQUILIBRIA

(1) In the original model with initial protection for mutants, four different types of maximally cryptic solutions were possible, featuring: (1) no investment in secondary defense: $t(0) = 0$; (2) some investment in secondary defense but not enough to make the prey aversive: $0 < t(0) < t_c$; (3) sufficient investment in secondary defenses to make the prey aversive $t(0) > t_c$; (4) no maximally cryptic solution exists; and each of these four situations could either exist in isolation or coexist with a conspicuous ($r > 0$) solution. Thus, there were eight different evolutionary regimes in the original model that featured initial protection for mutants. This situation is considerably simplified in our limiting case.

In the new ($a \rightarrow 0$) model, we can still get an equilibrium featuring maximal crypsis and no investment in toxic secondary defenses. From equation (11), this occurs whenever $f > k$. We can also get an equilibrium with maximal crypsis and investment in toxins that is not sufficient to be aversive (i.e., $t_o < t_c$). In both of these situations, the maximally cryptic equilibrium is the only equilibrium if it satisfies the condition for the solution to equation (17). If it does not, then there is no solution of this type.

It is also possible to have a maximally cryptic equilibrium when the investment in toxins is sufficient to be aversive ($t_o > t_c$). Indeed if $t_o > t_c$, then such an equilibrium is predicted always to exist. Further this equilibrium always coexists with a conspicuous ($r > 0$) equilibrium, because any time that the equilibrium value of t_o [as calculated from equation (11)] is greater than t_c, then a conspicuous equilibrium occurs. This is in fact a continuum of equilibria, with monomorphic values of any value of r greater than some threshold R being resistant to invasion by any mutant, where R satisfies

$$1 - qP(t - t_c)\left(v\left(\frac{D^2(R)}{D^/(R)}\right)\right) = 0 \qquad (19)$$

It is also possible to have no solutions of either of the above types; this occurs when neither of the inequalities in equations (15) and (17) are satisfied.

NONPOINT SOLUTIONS

In all of the solutions discussed so far, the value of θ is irrelevant provided all individuals adopt the same value. That is, at any equilibrium with $r > 0$, the population is monomorphic so as to take advantage of the positively frequency-dependent nature of aversion learning by predators. The original model also demonstrated the existence of a type of solution in which predators did not invest in toxins sufficiently to be aversive but there was no point solution for maximal crypsis. In this case, there was a potential solution in which individuals were conspicuous but were spread evenly across all θ values because frequency dependence now works against prey, because predators find attacking them to be a positive experience. Thus, they should seek to be as different from each other as possible.

If prey are aversive, then monomorphism is always best, and no such heterogeneous solutions exist. If the prey is nonaversive, then the solution will either be such a heterogeneous solution or a solution with maximum crypsis. Which of these is adopted depends on how the specific values given to parameters translate into the benefits of minimizing contact with predators through a maximally cryptic appearance versus accepting increased levels of exposure to predators in return for adopting heterogeneity of appearance to disrupt generalization of previous positive experiences by predators. It is likely that one of these benefits will always be better than the other, and so we conjecture that the two types of solution do not coexist for any given set of parameter values (although we have not rigorously proved this).

In the original model, we demonstrated that the nonpoint solution could be described by some function $P(r)$ that describes the distribution of prey individuals across different r-values. Solutions are bounded, such that $P(r) = 0$ for all $r \geq r_{max}$ for some r_{max}. For this solution to be an equilibrium, we require that the rate of attack is the same for all individuals regardless of their r-value; thus,

$$D(w)Q(I(w)) = D(0)Q(I(0)) \qquad (20)$$

for all $w \in (0, r_{max})$

and by the previous definition

$I(w)$
$$= H(t_1) \int_{r=0}^{r_{max}} D(r)P(r) \int_{\theta=0}^{2\pi} \left(\tfrac{1}{2\pi}\right)S\left(\sqrt{w^2 + r^2 - 2wrCos\theta}\right) d\theta \, dr \qquad (21)$$

Because a is irrelevant to the calculations above, we can be confident that such equilibria can exist in the new model also, although we have not delimited their properties or demonstrated their stability. For the present article, our interest is on the effect of the parameter a on these equilibria. First, we note that all other things being equal, the equilibrium level of toxicity declines as a tends to zero. So, we would expect $t < t_c$ to be more

commonly achieved in the limit $a \to 0$. However, for a given value of t, decreasing a increases the ease with which equation (16) can be satisfied, and so makes the $r = 0$ point solution more likely. Thus, these arguments do not give a clear answer as to whether nonpoint solutions will be more or less likely to occur as a tends to zero (i.e., whether it occurs over a greater or lesser range of parameter value combinations). The answer in any specific case will be critically dependent on the values given to the individual parameters.

Discussion

It is important first of all to be very clear about the biological underpinning of our definition of initial protection from predators. In our model, the parameter a describes the initial protection that the mutant gains from predation that allows it to flourish locally before predation pressure is felt. Specifically, it was assumed that although the mutants made up a negligible part of the whole prey population, they were numerous locally, so that any predator that encounters a mutant would have (on average) previously encountered mutants on a fraction a of its previous encounters, the residue of encounters being with resident types. This implies that there is a localized build up of the mutant phenotype before predation pressure is felt. This can occur through a number of biological mechanisms.

For example, there is considerable evidence that consumers do not immediately incorporate new prey types into their diet (Marples et al. 1998a; Marples and Kelly 1999; Kelly and Marples 2004). This phenomenon is called either dietary conservatism or neophobia, depending on the timescale over which the consumer's reluctance to sample extends. Such a mechanism would allow initial protection to a conspicuous mutant (Lindstrom et al. 2001a), which although detected would not be attacked. Providing the timescale of this aversion is long enough, this protection would allow the mutant to reproduce and the phenotype to spread in the population. However, eventually, either through familiarity and/or density-dependent effects, this aversion will break down and the mutant phenotype will be attacked. However, the initial aversion could allow mutant numbers to rise substantially at least at a local level.

Another mechanism is provided by territoriality of predators (Mallet and Singer 1987). Imagine that the landscape is overlaid by a mosaic of territories, within each of which a single predator has exclusive access to the local prey. If territories fall vacant for a period of time, say between the death of an owner and their replacement by another individual, then this will give a window of relaxation of predation pressure locally. During this window, if a conspicuous mutant arises, then this phenotype might spread in the local population by drift during the time when predation pressure is absent, such that the conspicuous phenotype might be locally abundant by the time a new predator establishes itself and predation pressure returns.

Yet another suggested mechanism is that the conspicuous phenotype is expressed through a maternal effect (Brodie and Agrawal 2001). The key underlying assumption here is that the initial genotypic mutation did not cause any change in the appearance of the bearer, and so no increase in its likelihood of being attacked. If that individual survives to reproduce, then the mutation is expressed phenotypically in the next generation. Thus, if the initial mutant has high fecundity and produces their offspring in a spatially restricted area, then this would lead to conspicuous coloration being locally relatively common when first expressed.

These three mechanisms are neither exhaustive nor mutually exclusive. All of them can lead to initial protection, the effectiveness of this initial protection in allowing the conspicuous mutant phenotype to become locally common would be enhanced both by high fecundity and by aggregation of offspring (Lindstrom et al. 2001b). It is important here to note that to be relevant to our model, aggregation does not require very tight clumping of offspring such that they are in physical contact in a single mass. Rather, all that is required is that they are spatially aggregated relative to the foraging range of a predator. So the eggs of a butterfly could be spatially aggregated from the viewpoint of an avian predator even if the butterfly lays only one egg per plant, provided the plants used by the butterfly are in close spatial proximity such that they all fall in the same bird's territory (say an area of several hundred square meters; for a full discussion of this, see Ruxton and Sherratt 2006).

Several recent publications have explored the potential for a relationship between the intensity of aposematic warning signals and the strength of the defense that is being signaled (Leimar et al. 1986; Summers and Clough 2001; Speed and Ruxton 2005; Broom et al. 2006; Darst et al. 2006a). Existing theoretical models, however, do not consider how starting conditions may lead to different evolutionarily stable strategies and, we argue here, the importance of evolutionary history has been largely ignored in explaining variation in aposematic traits. Comparison of our new and old models provides an interesting prediction: when aposematic prey receive initial protection from predation then investment in defense is linked to conspicuousness such that increased investment in defense is associated with increased conspicuousness; when no initial protection is available, then we predict investment in defense to be unrelated to conspicuousness.

Further, all other things being equal, the new model predicts that equilibrium levels of toxicity will be higher for prey given initial protection than those without. It might seem strange that the final level of toxicity that is maintained when the prey evolves to be monomorphic should be affected by the effect of predation on an uncommon morph. The answer is that the final level of toxicity in our model is an evolutionarily stable strategy, and to

be evolutionarily stable, the strategy must be resistant to invasion by mutant phenotypes that will initially start at low frequency. A strong level of protection from predation, as indicated by a high value of a, will increase the payoff for low-frequency morphs that are highly toxic, which in turn makes invasion more easy to achieve. In our new model, this drives the ESS to higher levels of toxicity.

Comparison of equations (13) and (14) demonstrates that conspicuous aposematic signals are less commonly predicted (i.e., predicted for a smaller parameter space) in our new model than in the original model. Hence, as expected, the model predicts that aposematic signals are less likely to evolve when initially rare aposematic mutants do not obtain some initial protection from predation. Although this has long been surmised for the case in which the mutant arises in a population with a fixed aversive level of secondary defense (Ruxton et al. 2004; Ruxton and Sherratt 2006), it has not been demonstrated before in the more general context in which investment in secondary defense and appearance are both freely evolving traits.

Note that our arguments above do not imply that aversive prey will always be predicted to signal aposematically by the new model. In fact, when the prey is aversive ($t > t_c$), the model predicts that there will always be two types of stable equilibria: one aposematic and one with maximum crypsis ($r = 0$). Further, the aposematic equilibrium is really an infinite set of possible solutions, in that there will be a minimum value of r that satisfies equation (12; which we term R), and all monomorphic populations with $r \geq R$ will be an ESS. The key prediction here is that when the prey are aversive, they can gain added protection from predators generalizing from previous aversive experiences, and so the only evolutionarily stable solutions have a monomorphic prey population that maximizes the effectiveness of this generalization. Thus, in nature we should not expect that maximally cryptic prey are necessarily nonaversive and we should not assume that more strongly signaling prey are necessarily more strongly protected (for a useful discussion of the empirical literature see Endler and Mappes 2004). The positive frequency dependence given by predator generalization means that we might expect different populations of the same species in very similar environments to develop very different signals simply through founder effects. However, within a local population (defined as those individuals linked by shared potential predators) we would expect strong selection pressure for homogeneity of appearance.

This selection may not, however, produce complete homogeneity if predators generalize across similar but not identical visual phenotypes, a phenomenon for which there is mounting empirical evidence (Darst et al. 2006b; Ham et al. 2006). Genetic effects (most obviously mutation and recombination) may also act to prevent complete homogeneity across a population (Exnerova et al. 2006).

It may at first seem strange that maximally cryptic solutions always occur for aversive prey but do not always occur if the prey are not sufficiently toxic to be aversive. The way to understand this is that aversiveness favors monomorphism because this allows the strongest protection through predator generalization. For exactly this reason, monomorphism should not be attractive to prey that are not aversive, because such prey would benefit from having a different appearance to previous palatable prey that the predator has encountered. Thus, nonaversiveness favors the nonpoint solution in which prey are equally spread across all θ values, to minimize the effectiveness of predator generalization. For example, within-population variation in appearance should disrupt search image formation by predators (see discussion in Punzalan et al. 2005). However, a monomorphic maximally cryptic prey population can still be found for some parameter values in which the benefits of reduced encounter rate with predators is greater than the benefits of reduced predator learning through having a population that is heterogeneous in appearance. Clearly, in such a situation, a monomorphic population with $r > 0$ would never be the best strategy, and is thus never predicted by our model when prey are nonaversive.

In our model, we describe the appearance of each prey individual using polar coordinates, with r describing the effect of appearance on conspicuousness and θ describing the effect of appearance characteristics that have no effect on conspicuousness. Our reason for adopting polar coordinates was to capture the idea that crypsis strongly constrains the appearance of individuals, and by relaxing crypsis prey could achieve a much greater variety of appearances. Effectively, we are assuming that there are many more ways to be obvious than there are ways to be cryptic. Indeed, by adopting polar coordinates to describe appearance, we have assumed that maximally cryptic prey (with $r = 0$) are monomorphic by default, and the only way to become polymorphic is to give up some of the benefits of crypsis. The more the benefits of crypsis are relinquished (the higher r), the more different two morphs of the same conspicuousness (same r) can appear from each other. Thus, we see the essential trade-off of the nonpoint solutions that causes them to have nonzero r-values, and also to be bounded above by a maximum r value. The larger the r values that the population use, the more different in appearance individuals can be from each other and so the weaker will be predator learning; but the higher r is, the more frequently predators will encounter the prey.

Our polar coordinates are certainly a simplification of reality, but there is very little empirical understanding of how different in appearance two prey items can be and still both be maximally cryptic, or (more generally) still have similar conspicuousness. Empirical testing of our basic assumption that increased levels of crypsis can only be bought at the cost of increased constraint on individual appearance would be very welcome (Tullberg et al.

2005). Our model considers a very simplified situation in which the predator only encounters one prey species; in reality it is likely that predators will encounter a range of different prey types that differ in both appearance and defense. However, if we are correct that maximizing crypsis involves accepting strong restrictions on appearance, then it is likely that two maximally cryptic species that share the same environment may have very similar appearance to each other, such that they can be confused for each other by a potential predator.

This will complicate the model if, as is likely, the two prey species differ in their defense levels, because it introduces another factor into the model—the likelihood of the predator misidentifying an individual of one species as belonging to another. The consequences of this for selection pressure on prey appearance will depend on the fine detail of the predator's learning and generalization behaviors. Clearly an aversive prey may pay a cost if it is mistaken for a palatable prey type, whereas a palatable prey type may be prepared to adopt a monomorphic conspicuous appearance if this buys them protection through being mistaken for an aversive species. This is the basis for Batesian mimicry (Bates 1862; Brower et al. 1964). It may be that two aversive species can benefit from sharing the same appearance (the basis of Mullerian mimicry; Muller 1879), although this may depend on the fine detail of how predators generalize between prey of similar appearance but different levels of defense (e.g., Langham 2004). Finally, it may be that aversive prey find cryptic appearance less attractive if this increases the likelihood of being misidentified as another species of nonaversive prey (Sherratt and Beatty 2003).

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