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Automimicry and the evolution of discrete prey defences

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We consider the neglected question of how secondary defences of prey animals evolve if they are discontinuous in nature, being either present or absent, or expressible over a limited number of levels. We present a novel computer model that evaluates the conditions in which defended mutant prey may (1) fail to rise above nontrivial levels within a population, (2) reach values close to fixation, or (3) find some evolutionarily stable strategy (ESS) frequency between these two situations. Undefended prey that coexist with defended conspecifics are known as automimics. One finding is that automimicry can be an ESS over a range of conditions, but especially when prey are relatively cryptic and secondary defences are very effective at deterring predation. Evolutionarily stable automimicry emerges from the interplay between the direct benefits of costly defences in surviving individual attacks by predators and frequency-dependent benefits conferred on all prey, from a reduction in the rate of attack on all identical-looking prey. When, in contrast, secondary defences have continuous variation, the result is effectively a monomorphic state of defence across the population. Thus the degree and kind of variation that a defence takes has a profound effect on its initial evolution. We discuss the interesting possibility that mixed ESSs may help explain some examples of variation in prey secondary defences. © 2006 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2006, **87**, 393–402.

ADDITIONAL KEYWORDS: anti-predator traits – aposematism – mimicry – warning signals – within-population variability.

INTRODUCTION

The term ‘aposematic’, coined by Poulton & Sidgwick (Poulton, 1890), refers to a prey that has both an effective secondary defence (such as a toxin, sting, sharp spine, tough integument or shell, or defensive teeth or claws) and an advertisement of that defence in the form of a warning display. Whilst the evolution of warning displays has been the focus of considerable attention in aposematism studies (see recent reviews in Lindström, 1999; Speed, 2003), the existence of secondary defences is usually taken for granted (e.g. Harvey *et al.*, 1982; Sillén-Tullberg & Bryant, 1983; Servedio, 2000; Brodie & Agrawal, 2001; Speed, 2001; Sherratt, 2002, e.g. Yachi & Higashi, 1998). Thus it is often explicitly assumed that prey were cryptic *and* defended before evolving some kind of warning signal. However, focusing on the mechanisms that drove the evolution of defensive advertisement may exclude consideration of a pivotal event in the evolution of aposematism, namely the evolution of the secondary defence that is to be advertised. Secondary defences may be costly to generate and maintain and hence their evolution may need special consideration (see data and discussions relating to chemical defences in Cohen, 1985; Rowell-Rahier & Pasteels, 1986; Bjorkman & Larsson, 1991; Bowers & Collinge, 1992; Dobler & Rowell-Rahier, 1994; Camara, 1997; Grill & Moore, 1998; Mebs, 2001; Zalucki, Brower & Alonso, 2001). In particular, if defences often evolve before aposematic displays in prey animals, there is a paradox: why should prey invest in costly secondary defences if they are already well-protected by crypsis?

There are two general explanations to resolve this paradox. The first explanation is via preadaptation.

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Thus, for example, a prey species may already possess a trait that happens to provide some protection against a newly encountered predator. Some chemicals may, for example, be important in intraspecific signalling, and may also deter predators (see Discussions in Weller, Jacobson & Conner, 1999). Similarly locomotor behaviour and mechanical properties could have some function as a secondary defence even though they were not initially selected for this role.

A second class of argument is that defences evolve or emerge *de novo* by genetic mutation or some other change. With chemical defence, genetic mutation may render prey tolerant of toxin-conferring food materials, or provide new secondary metabolites that are toxic to predators. With mechanical and other defences mutation may cause the development of structures such as spines, or enable changes in locomotor behaviour that facilitate escape. In some circumstances defences could emerge *de novo* without genetic change; for example, prey may have a choice of acquiring a secondary defence by behavioural modification, rather than by genetic mutation, choosing, for instance whether to feed on certain materials or to acquire certain symbionts.

In this paper we address the evolution of this second class of secondary defence, that which does not arise through preadaptation. Perhaps surprisingly, there are very few theoretical treatments that consider how costly defences may evolve in this context. In a model of major importance Leimar, Enquist & Sillén-Tullberg (1986) assumed continuous variation in prey defences, and modelled the responses of predators that learn about defended prey and generalize between similar forms. Leimar *et al*. (1986) showed that for continuous variation in defence, there would be one single evolutionarily stable strategy (ESS) value of defence for a given level of exposure (and of localized family clustering).

However, it is possible that defences are not subject to continuous variation, but instead may come in a number of discrete forms. Most obviously, at the initial evolution of a defence, a mutation may confer a secondary defensive trait of arbitrary value, in which case individuals may be characterized by the presence/absence of a defence. Furthermore, it has been demonstrated repeatedly, for example, that many prey gain chemical defences from food materials. Hence changes in diet can add or remove toxic defences (e.g. Edmunds, 1974; Brower & Glazier, 1975; Bowers, 1980; Berenbaum & Miliczky, 1984; Ritland, 1994; Pasteels *et al.*, 1995; Moranz & Brower, 1998; Tullberg, Gamberale-Stille & Solbreck, 2000). Some species have gut-mediated toxicity, so that they are only chemically defended when their guts contain toxic materials (e.g. Sword, 2002). Finally, individuals in many species may have the option of utilizing costly behavioural responses (e.g. secretion of a toxic substance), so that for any given level of threat a population may contain individuals that secrete and others that do not.

Guilford (1988, 1994) suggested that when secondary defences are costly they may in some circumstances be subject to 'cheating' such that the evolution of defence may be characterized by mixed ESS states, in which defended and undefended conspecifics coexist at an ESS frequency with equal fitness. Guilford's suggestion has been influential, inspiring some researchers to look for the existence of cheats within chemically defended species (e.g. Holloway *et al.*, 1991). A situation in which prey look exactly alike but vary in defensive levels is known as automimicry (Brower, Brower & Corvino, 1967). Recent empirical studies show that understanding automimicry may be essential in the comprehension of aposematic stability (Gamberale-Stille & Guilford, 2004). Most often the term 'automimicry' is used to refer to variation in conspicuous, aposematic prey, but the same principle, and the same evolutionary considerations, apply when prey are relatively cryptic. As we describe in this paper, a mixed ESS solution may be especially likely for discontinuous defences that emerge in cryptic species.

The possibility that a stable polymorphism exists for levels of secondary defence has received very little theoretical attention (though see an excellent example for modular plants in Till-Bottraud & Gouyon, 1992), but has important implications for the initial evolution of secondary defences. In addition, automimicry, in one form or another, is very common, especially when the secondary defences are toxins. Automimicry implies that the predator cannot easily differentiate between defended and undefended individuals, and this requirement is more easily met for toxins than for externally visible defences such as spines. Bowers (1992), considers the situation of intraspecific variation in defence to be 'probably very common, if not ubiquitous, in unpalatable insects'. Other theoretical treatments of discontinuous defences consider only the levels of automimicry that can be sustained without totally negating the protection of defended prey (e.g. Brower, Pough & Meck, 1970; Pough *et al.*, 1973) but do not consider that the presence of automimicry may itself be stable.

In this paper, therefore, we describe a model that evaluates the ecological parameters that may effectively retain or exclude a mixed ESS within a prey population. We describe a stochastic model in which predators are inhibited from attacks for a period after an encounter with a defended prey, and prey can vary in (i) their probability of surviving an attack, (ii) the extent to which they cause inhibition of attacks in predators, and (iii) other parameters such as costs of defences, population size and time, that must be survived until reproduction. We demonstrate the conditions under which a discontinuous defence is or is not likely to increase in frequency in a population, delimiting the factors that may determine whether or not the stable point is effectively fixation or some mixed ESS value. We then discuss the evolution of defences in cryptic and other prey.

EVOLUTIONARY SIMULATION MODEL

We consider a prey population with a very simple life-history strategy: asexual reproduction occurring in discrete generations. The generation time T is fixed. After this time, all survivors reproduce (clonally) then die, their progeny beginning a new generation. The population size at the beginning of each generation is a constant (N_1). Individuals are identical in appearance, with their conspicuousness being described by a parameter C. This can be interpreted as the rate at which an individual encounters the predator. For simplicity, we assume only a single predator, but our results are not sensitive to this assumption. Individual prey items can potentially differ in one intrinsic characteristic: their level of defence (D), such that the genotype of individual i is fully specified by the value of D_i.

We begin each generation at time $t = 0$, with a fixed initial number of individual prey items, N_1. We first calculate the time (t_1) until the predator first encounters a prey item. This is simply a random number drawn from a negative exponential distribution with mean value equal to the inverse of the total encounter rate with all prey alive at that time:

$$t_1 \to \exp\left(-\frac{N_1}{C}\right).$$

We then move forward to time $t = t_1$, and stochastically select the prey individual that the predator encounters, with each having equal probability.

When the predator encounters individual i, the outcome is dependent on the defence level of that individual (D_i) in two ways. Firstly, the time taken in the encounter increases with defence level. For simplicity we define defence level in this way: if the predator encounters an individual with defence level D_i, then it takes a time D_i for the interaction with that prey item to be concluded. During this time, no encounters with other prey items can occur. This can be interpreted in a number of ways. For example, D_i can be the time needed to overcome a physical defence such as spines or a tough integument. Alternatively, D_i can be interpreted as the time needed to recover physiologically from ingested toxins during which searching for prey is curtailed. Avoidance for a defined period after an attack is a common assumption in many models of predators and mimicry, including automimicry (e.g. Brower *et al.*, 1970; Pough *et al.*, 1973; Bobisud & Potratz, 1976; Speed & Turner, 1999). However it is interpreted, if the first prey encountered (after time t_1) is individual i, then that encounter takes a further time D_i, so the predator begins looking for further prey at time $t = t_1 + D_i$.

D_i also determines whether individual i survives the encounter with the predator. We expect that the probability of surviving an encounter S_i should increase with D_i, and assume the functional form:

$$S_i = 1 - \exp(-sD_i),$$

for some positive constant s (see Gamberale-Stille & Guilford, 2004). The survivorship of a given encounter is determined stochastically.

If the first prey item encountered in a given generation survives, then the number of prey items from which the second encountered individual will be drawn randomly remains unchanged ($N_2 = N_1$), otherwise the first encountered individual will be removed from the population and $N_2 = N_1 - 1$ remain. We then proceed to calculate the further time until the predator encounters a second prey item, drawn stochastically from the appropriate negative exponential distribution:

$$t_2 \to \exp\left(-\frac{N_1}{C}\right).$$

The identity of this individual is obtained stochastically as before, using equal probabilities for all individuals still alive.

The duration and outcome of this second interaction is determined stochastically, exactly as for the first interaction. We continue in this fashion until the end of the generation (i.e. when time $t > T$). At this point there will be some number of individuals surviving, N_i, and we will select N_1 progeny from these, to begin the next generation (resetting t to zero). We assume that the probability of an individual reproducing decreases with its level of defence (representing the idea that defences are costly). Again, we assume a simple exponential relationship, with the reproductive potential of individual i given by:

$$R_i = \exp(-cD_i).$$

Setting c to zero assumes no cost to defences; increasing c increases the cost of defences. The probability that individual i is the parent of the j^{th} offspring is simply:

$$\frac{R_i}{\sum_{j=1}^{N_i} R_j}.$$

An individual is selected randomly (with replacement) and independently to be a parent for each of the N_1 offspring. The final thing that we need to define is how we determine the genotype of each offspring. The genotype of offspring j $\{D_j\}$ will be determined in part stochastically and in part by the genotype of its parent $\{D_i\}$. If we assume that the defence can take only two discrete values $\{D_{low}, D_{high}\}$, then offspring will simply inherit the same value as their parent with probability $(1 - \mu)$ and the opposite value with probability μ (where μ is a simple constant). In the case where the values that D can take are continuous, then we assume that individuals inherit their parent's value of a given characteristic plus a small perturbation drawn from the uniform distribution $[-\varepsilon, \varepsilon]$, subject to re-sampling to ensure that values remain positive.

In order to run a simulation, the number of individuals at the start of a generation N_1 must be specified, and D_i values given to all these individuals. We need to specify the generation time T and the number of generations over which we want the simulation to run. We expect the distribution of D-values to settle down to equilibrium values (regardless of the starting values) providing we allow a sufficient number of generations to elapse. We also need to supply values for the constants in the survival and reproductive and cost of defence functions (s and c, respectively), and the mutation rate parameter (either μ or ε).

RESULTS

We will first explore the ecological situation in which there are only two possible morphs, one of which is undefended ($D_{low} = 0$), and the other of which is defended strongly ($D_{high} = 5$). We assume that no intermediate forms are possible. If we set the effectiveness of defence parameter (s) to 0.12, then undefended prey never survive an attack, whereas defended prey have a 45% chance of surviving an attack. If we set the generation time (T) to 200, then we can see that the consequence for the predator of attacking a defended prey item is that it loses foraging time equivalent to 2.5% of the prey's generation time. We assume that the carrying capacity of the prey (N_1) is 200 individuals, and that the conspicuousness of both morphs is identical: $C = 0.005$. This means that (at carrying capacity) the mean interval for the predator between beginning to search for prey and encountering a prey item is 1 time unit, or 0.5% of the prey's generation time. We set the cost of defence parameter (c) at 0.05, so that the reproductive potential of a defended prey individual that survives to the end of a generation is 78% that of a surviving individual that did not invest in defence (see e.g. values in Hetz & Slobodchikoff, 1990).

If we start with a small inoculum of five defended individuals (and assume a small probability of mutation (μ) of 0.005), then a typical trajectory of the number of defended individuals in the population over time is as shown in Figure 1. Because of the stochastic nature of the model, different simulations of the same model produce slightly different trajectories, but the quantitative trend for these parameter values is always as shown in Figure 1. There is an initial transitory period of between 50 and 100 generations (while the behaviour of the population is still strongly influenced by the starting population) before the system settles down to its final dynamics. The same final dynamics are reached no matter what the initial state of the population and no matter what the rate of mutation (μ). That is, other simulations (not shown) demonstrated that the final dynamics shown in Figure 1 would be reached by models with the same parameter values but which started with any fraction of the initial population being defended, including 0 and 100%. The mutation rate affects only the speed at which the system moves towards the final dynamics. Even when the mutation rate is zero, differential frequency-dependent fitness of the two morphs still causes the same final dynamics to be reached, providing that the initial numbers of each phenotype are sufficiently high to avoid demographic stochastic extinction of either type during the initial transient phase.

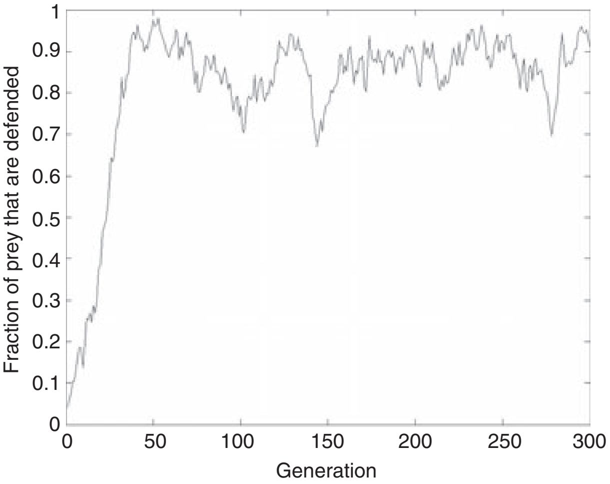

Figure 1. Time series of the model for the base-line parameter values showing a transient phase then final intrinsic dynamics, which feature fluctuations in the frequencies of the two morphs but continual polymorphism. ($D_{low} = 0$, $D_{high} = 5$, $C = 0.005$, $N_1 = 200$, $T = 200$, $s = 0.12$, $c = 0.05$, $\mu = 0.005$).

The final dynamics are characterized by polymorphism of defence. Although defended individuals form the majority of the population for these parameter values, they do not grow to fixation and exclude the undefended types. This is not simply a function of the mutation rate, which is very low, with an average of one mutation occurring every five generations. Rather, the polymorphism is a direct consequence of the intrinsic behaviour of the model. The polymorphism in defence occurs because prey gain protection from predators in two ways. First, if an individual is attacked by the predator, then if it is defended this gives it a chance of surviving that attack. Second, the rate at which an individual (whether defended or not) faces attacks decreases as the number of defended individuals in the population increases, because the predator pays a time penalty for attacking a defended item, reducing the time it has in a given generation to attack prey.

When the frequency of defended prey in the population is low, then attacks are frequent and the cost of defence (paid in reduced reproductive potential) is more than compensated for by increased survival. Hence, defended individuals are at a selective advantage. Conversely, when defended individuals are very frequent in the population, then the predator's attack rate declines very significantly. Now, the cost of defence is less attractive, since the probability of never being attacked is relatively high. Hence, when defence is common in the population, undefended individuals find themselves at a selective advantage and increase in frequency over time. These selective pressures balance at an intermediate frequency of defended prey, essentially the theoretical mixed ESS point, and polymorphism persists. The population sometimes displays strong fluctuations in the frequencies of the two morphs because of the stochastic nature of the model. If the population deviates from the point of equilibrium then selection restores the population to equilibrium and the polymorphism persists (see also Guilford, 1994).

We now explore how the model is affected by changing parameter values. As we study one value, all the other parameters retain their baseline values (as described above and used in Fig. 1). First we consider the survival advantage of defence. As the parameter s increases (but the inhibitory effects on predators remains fixed), so the probability that a defended prey item survives an attack increases, and there is a consistent increase in the fraction of defended prey with increasing s (Fig. 2A).

Increasing the reproductive cost of investing in defence (c) decreases the frequency of defended individuals in the population (Fig. 2B). Slightly less obvious is that increasing the aversive effect of the defended prey (D_{high}) leads to a reduction in the frequency of defended prey in the population (Fig. 2C). Increasing D_{high} reduces the likelihood that any prey item, whether defended or not, will be the victim of an attack. In this case, the improved survival of an attack that goes along with an increase in D_{high} for defended prey does not compensate for the reduction in reproductive potential. Similarly, increasing the maximum size of the prey population (N_1) decreases the benefit from defence (through a dilution of risk effect) and so the fraction of defended individuals decreases (Fig. 2D). As generation time T increases, so defence becomes more attractive because the balance between survival and reproduction shifts towards survival, because individuals must stay alive for a longer time before having the opportunity to reproduce (Fig. 2E). A similar argument explains why the fraction of defended individuals in the population increases with the frequency with which individuals are encountered by the predator (C) (Fig. 2F). We should point out that small population size and nonzero mutation rate mean that the proportions in the figures are all kept away from absolute values of 0 or 1, even when one of the strategies is clearly better. Notice, that automimicry does not require one of the defence levels to be zero; Figure 3 demonstrates a persistent polymorphism between a strongly defended morph ($D_{high} = 5$) and a moderately defended morph ($D_{low} = 3$).

From the results above, automimicry is predicted under a wide range of ecological circumstances. However, it is important to emphasize one key aspect of the model considered so far, and that is that the levels of defence are discrete (either of two values considered in all the simulations so far). In some ecological circumstances, defence can vary continuously. Our model can investigate this situation also, and sample results are shown in Figure 4. The key conclusion is that, although there is small between-individual variation in defence, this is a result of the noise introduced into the system by the process of mutation. Further simulations (not shown) demonstrated that the smaller the mutation size parameter (ε), the smaller the variation. Thus where Figure 1 shows a stable polymorphism of defended and undefended individuals, Figure 4 shows a population with very little between-individual variation in defence once the final dynamics have been reached. The only difference between the models used to generate the two figures is that defence can take only two discrete values in the model of Figure 1 but can vary continuously in that of Figure 4. Hence, a necessary condition for automimicry to be predicted in our model is that levels of defence are discrete.

DISCUSSION

A principle aim of this paper was to examine under which conditions defences may evolve if they are discontinuous in nature. In a scenario of presence/absence of a defence, the simulations allow us to identify factors that determine which prey populations will have effectively no defences, and which will have very high, virtually monomorphic levels of defended individuals or some stable frequency of defended individuals between these levels.

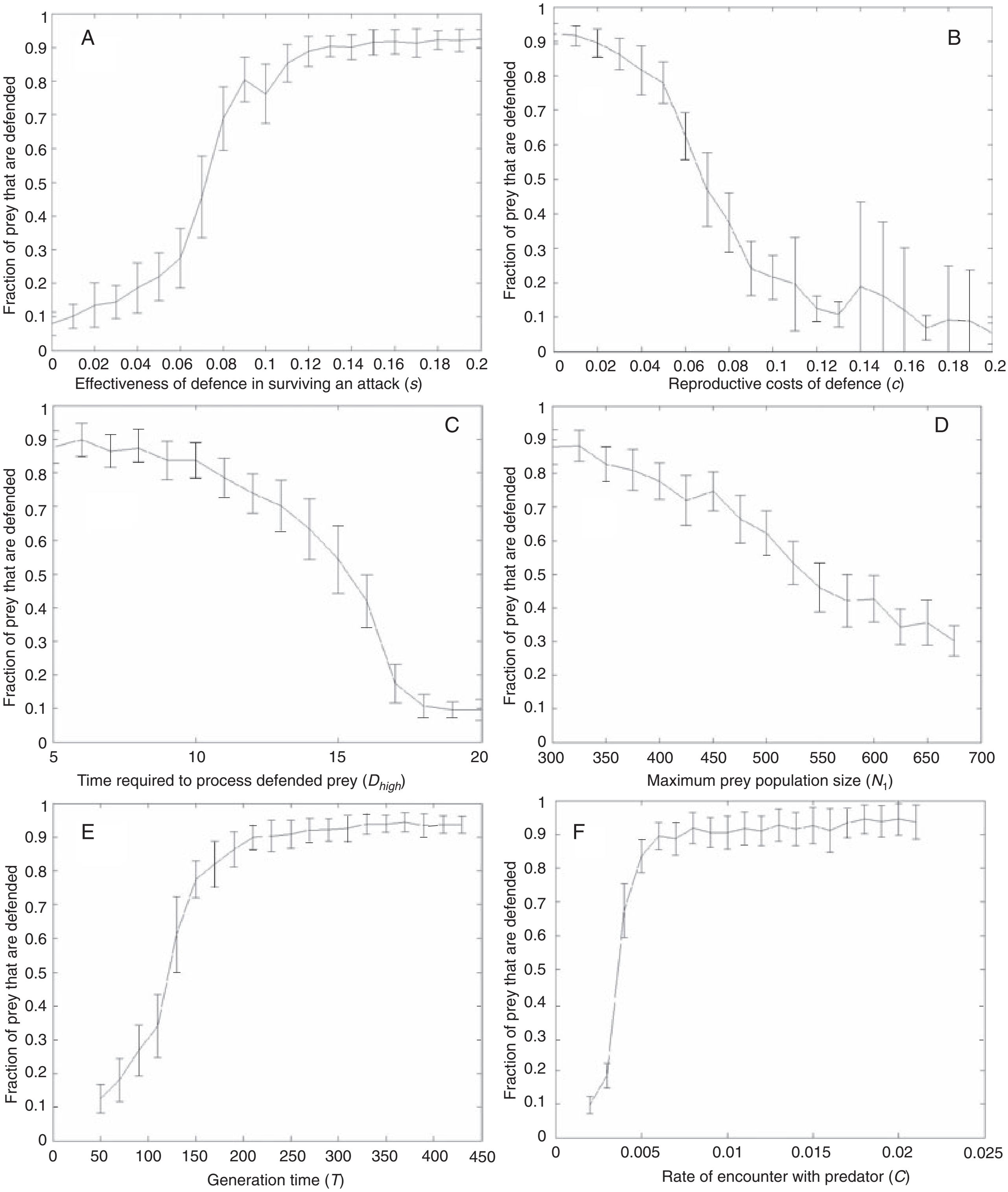

Figure 2. Mean and standard deviation (across the population) of the fraction of prey that are defended at the start of generations 400–500 of simulations with different values for (A) the constant controlling the effectiveness of defence for surviving an attack by the predator (s), (B) the reproductive cost of investing in defence, controlled by parameter (c), (C) the length of time it takes a predator to recover after attacking a defended prey individual(D_{high}), (D) the maximum size of the prey population (N_1), (E) the generation time of the prey (T), and (F) the rates at which prey encounter predators (C). The values taken by other parameters are as in Figure 1.

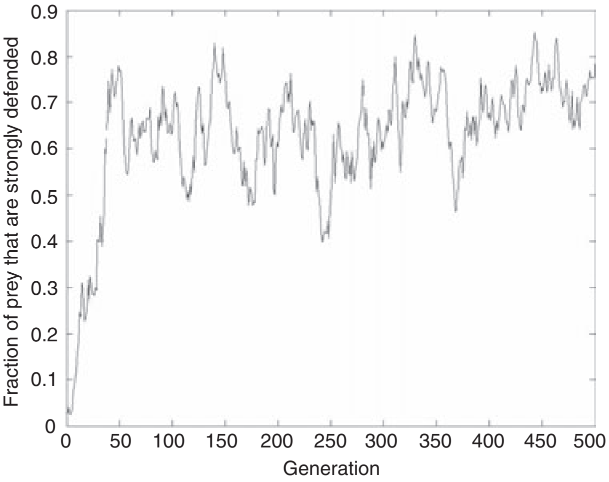

Figure 3. Time series of the model for the base-line parameter values expect that the lower level of defence is nonzero, showing a transient phase then final intrinsic dynamics, which feature fluctuations in the frequencies of the two morphs but continual polymorphism. ($D_{low} = 3$, $D_{high} = 5$, $C = 0.005$, $N_1 = 200$, $T = 200$, $s = 0.12$, $c = 0.05$, $\mu = 0.005$).

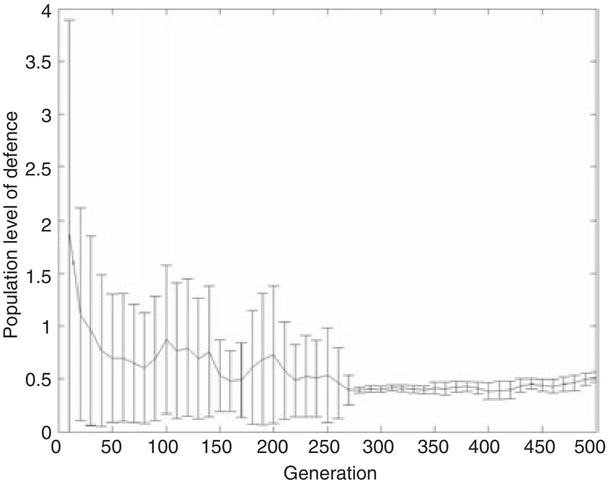

Figure 4. Example with continuous defence: mean and standard deviation (across the population) of the population-wide level of defence (the D_i values) as a function of generation. Parameter values are as in Figure 1, except that D_i can now vary over a continuous scale. $\varepsilon = 0.01$.

Factors that lead to predictions of no, or very low proportions of, defended prey include: (1) low probability of surviving an attack; (2) high cost of defences to prey; (3) large inhibition by the defence on attacks by predators; (4) large population sizes; (5) short generation times; (6) a low rate of encounter with predators (low conspicuousness and/or a small number of predators).

Thus cryptic undefended prey may be invaded by cryptic forms with secondary defences, but these defended prey may remain at a low stable frequency – unless there are low costs to the defence, the defences provide very high levels of survival, generation times are relatively long, or there is a relatively high abundance of predators in the environment.

Conversely, if we increase the probability of surviving an attack (without increasing D), and/or increase the generation time and the probability of encounter with a predator, then we raise the fraction of defended individuals in a population. If we decrease the cost of a defence, and/or the extent that an attack on a defended prey causes inhibition of further attack, and/or the population size, we similarly expect a rise in the proportion of defended prey.

All other things being equal, any factor that increases the inhibition of predators to attack leads to a decreased equilibrium level for the defended form, provided that defence is costly to generate and maintain. Mixed ESS results are not limited to situations with presence/absence of a defence; when there is a difference in defensive level between two forms of a prey, mixed ESS is also possible (Fig. 3). However, mixed ESS values do not result in our model if there is continuous variation in defensive levels (Fig. 4). Hence, there is an apparent difference in predictions between a discrete defence model (with mixed ESSs) and a continuously variable model (without mixed ESS results) in Leimar *et al*. (1986). This is an important point to clarify. Holloway *et al*. (1991), for example, performed an excellent evaluation of variation in defences in the seven-spot ladybird *Coccinella septempunctata* on the grounds that it might show a mixture of defended and undefended individuals in accordance with Guilford's (1994) argument. However, this animal shows continuous variation in defensive levels, so a mixed ESS of defence/no defence is not predicted by our model and was not in fact observed.

In summary, we suggest that the nature of a secondary defence, and in particular whether it is continuous or discontinuous in nature, may have a profound affect on its initial evolutionary dynamics. However, the generality of the predictions of our model will require further investigation, as some game-theory models (developed in a different context to ours) with continuous trait variation have shown the development of stable polymorphisms (e.g. Doebeli, Hauert & Killingback, 2004).

VARIABILITY OF EVOLVED SECONDARY DEFENCES

Whether simple discontinuous models apply to evolved secondary defences is an interesting but complex question that probably needs to be answered by a systematic case-by-case investigation (e.g. see Holloway *et al*., 1991). An initially evolved discontinuous defence may be affected by the subsequent invasion of alternative defence alleles and the accumulation of genetic modifiers, which may move a prey population closer towards continuous expression of a defended trait. When this is the case, a continuously variable model like that of Leimar *et al*. (1986) may be more appropriate.

However, we note that the simple monomorphic ESS result predicted in the model of Leimar *et al*. (1986) sits uneasily with the repeated observation that variation in secondary defences is common, especially in cases of chemical defence (see review in Ruxton, Sherratt & Speed, 2004). Hence we raise the interesting possibility that in some defended species, the presence of automimicry is affected by selection favouring a stable polymorphism, although there are a number of other potential explanations for the widespread observation of variation in defence within individuals in a population.

Additional reasons for variation in defences of evolved populations include: (1) genetic variation within populations that cause different levels and profiles of (for example) toxins, which may arise, for instance, because of pleiotropy and linkage disequilibrium; (2) variation in individual life-history circumstances. Thus, suppose that a set of genetically identical prey develop and live in different environments, we may expect them to show individual variation in defensive traits, especially if defences are costly and utilize particular kinds of resources. Prey in areas with abundant resources may gain higher levels (and different kinds of cocktails) of defensive chemicals than do those that develop in areas of poor resources. We speculate that some chemically defended prey may even be sensitive to predatory risk during development and that this is reflected in the level and type of toxins that they acquire, in a manner analogous to the inducible physical defences reported in aquatic organisms. Furthermore, (3) prey populations may show variation in defences because predators have frequency-dependent preferences for individuals with familiar toxins (Pasteels & Gregoire, 1984) or (4) because larval prey living on defended host plants are preferentially targeted by parasitoids (Gibson, 1984). Thus, there is a range of factors to explain variation in defensive traits in populations with established secondary defences; but mixed ESSs may be one that has been unduly neglected. Further work will be required to evaluate the relative importance of these different traits for the distribution of variation seen in the natural world and as candidate explanations for specific examples of automimicry.

It is important to remember than these candidate mechanisms are not mutually exclusive. For example, host-plant characteristics may affect toxicity both in caterpillars that feed on them and in the adult butterflies that these caterpillars become. Variation in toxicity (in both caterpillars and adults) may stem from variation in the chemical composition of the host plants. This variation may simply be a result of environmental variation in the plants available locally, but variation can also be influenced by selectivity by females. Hence, for example, the hereditary variation considered in this paper could be generated by genetically determined host-plant selectivity by egg-laying females, with some genetic combinations selecting for a preference for a host species that confers toxins on the caterpillar and some combinations selecting for another host-plant species that does not. This may not necessarily lead to automimicry in caterpillars if predators can use the host plant as a cue to determine the likely toxicity of any caterpillars on it, but when caterpillars become free-flying adults this cue is lost and automimicry may emerge.

Our model assumes very simple behaviour by the predator, and it would be appropriate, when evaluating the importance of the mechanism described here, to explore its robustness to increasingly flexible predatory behaviour. For example, predators are likely to have alternative prey types available to them, giving them the option (on either evolutionary or behavioural timescales) of eliminating from their diet prey types with a high proportion of defended individuals. This action by the predators could encourage the spread of automimics in the prey population, although the proportion of automimics could not grow too large before it became profitable for the predator to re-incorporate that prey type into its diet. Hence, automimicry is likely to be maintained by a dynamic balance between selection pressures on both prey and predators. If a prey type shows aposematic colouration to warn of toxic defences, then predators must often learn to associate the aposematic signal with unpleasant experiences. At first sight, undefended automimics might be expected to make this learning process more challenging to predators, since the same signal is associated with different types of experience (palatable and unpalatable prey), but variation in defence can lead to accelerated learning in some circumstances (Skelhorn & Rowe, 2005). Thus the effect of automimicry on predator learning is far from obvious, and more research is warranted.

CONCLUSIONS

We highlight in this paper an important distinction in terms of evolutionary dynamics between defences with continuous variation in expression and those with discontinuous variation. Should a secondary defence emerge which is 'all or nothing' (or in two unequal states of defence), there are a number of circumstances in which a stable polymorphism may emerge, especially if the prey is cryptic. In contrast, if there is continuous variation, then the population will tend towards monomorphism. Stable polymorphism may have characterized the initial evolution of a number of defences. Whether it applies to defences in evolved populations is an open question but is a possibility worthy of consideration.

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