

Warning signals and predator–prey coevolution

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Theories of the evolution of warning signals are typically expressed using analytic and computational models, most of which attribute aspects of predator psychology as the key factors facilitating the evolution of warning signals. Sherratt provides a novel and promising perspective with a model that considers the coevolution of predator and prey populations, showing how predators may develop a bias towards attacking cryptic prey in preference to conspicuous prey. Here, we replicate the model as an individual-based simulation and find, in accordance with Sherratt, that predators evolve a bias towards attacking cryptic prey. We then use a Monte Carlo simulation to calculate the relative survivorships of cryptic and conspicuous prey and stress that, as it stands, the model does not predict the evolution or stability of warning signals. We extend the model by giving predators continuous attack strategies and by allowing the evolution of prey conspicuousness: results are robust to the first modification but, in all cases, cryptic prey always enjoy a higher survivorship than conspicuous prey. When conspicuousness is allowed to evolve, prey quickly evolve towards crypsis, even when runaway coevolution is enabled. Sherratt's approach is promising, but other aspects of predator psychology, besides their innate response, remain vital to our understanding of warning signals

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1. INTRODUCTION

Nature is rich with organisms that display bright warning colorations. Although such displays intuitively appear to be an honest indication of a defence mechanism, biologists have long puzzled over their evolutionary origins. Specifically, interest stems around finding conditions under which defended organisms will evolve conspicuous, rather than cryptic, colorations. Why, for example, do bees flaunt bright stripes when a more cryptic form would help to hide them from predators? In particular, if we assume that ancestral bees were cryptic, what was the evolutionary advantage for a conspicuous mutant?

Theories of the evolution of warning signals are typically expressed, using analytic and computational models. Most models attribute aspects of predator psychology (e.g. learning and forgetting rates) as key factors facilitating the evolution of warning signals (e.g. Harvey *et al.* 1982; Sillén-Tullberg & Bryant 1983; Leimar *et al.* 1986; Guilford 1990; Yachi & Higashi 1998; Servedio 2000; Speed 2001). Such models are typically receiver oriented, i.e. they focus on predator response to the presence or absence of warning signals. The models generally include only a single predator, and predict the evolution of warning signals over a relatively narrow range of conditions. For example, Speed (2001) predicts generally that warning signals will evolve when predators, equipped with the ability to learn, have a better memory for aposematic prey than for cryptic prey, or when predators are neophobic and have some degree of forgetting.

Sherratt (2002) provides an innovative perspective on the evolution of warning signals by considering coevolving predator and prey populations. The model's predators are deterministic, in that they have a fixed behavioural strategy

over their lifetime, and cannot learn from experience. For both cryptic and conspicuous prey, each predator has a fixed policy of either attacking or avoiding.

The model stands out from other approaches in several ways: it allows predators and prey to coevolve, it does not primarily rely on predator psychology as an explanatory factor, and it is the first to acknowledge that the decision of one predator can, through evolution, influence the decisions of future predators. Thus, it marks a shift in emphasis for warning signal research to examining predator–prey coevolutionary approaches. However, the ambitious aims of Sherratt's work, coupled with its mathematical framework, have necessarily led to a focus on the selective pressures affecting predators rather than prey. This leaves room for an individual-based model in which both sides of the coevolutionary relationship can be thoroughly addressed.

In this paper, we first present a description of Sherratt's model. Second, we present an individual-based simulation model as a reworking of his analytic model, and consider prey survivorship over a range of conditions so as to further explore the situations under which conspicuous colorations are evolutionarily advantageous. We then present extensions of the model where: (i) predators have continuous attack strategies rather than being restricted to two or three behavioural options; (ii) prey conspicuousness can evolve; and (iii) 'runaway coevolution' is enabled, by dropping the assumption that migrating prey will be drawn from a fixed distribution of cryptic versus conspicuous and undefended versus defended individuals.

2. SHERRATT'S MODEL

Sherratt's (2002) model assumes a world where a diverse range of prey migrate to a locality inhabited by a population of predators. Prey are assigned a level of conspicuousness measured by p , their probability of detection by predators. In the analytic model, all possible values of p are considered,

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whereas in a subsequent simulation version of the model, prey are either highly conspicuous ($p = 0.9$) or highly cryptic ($p = 0.1$). This detectability parameter represents how easily a prey item can be perceived as distinct from its background (Guilford & Dawkins 1991). An individual prey item entering the locality is defended with probability $1 - q$ or undefended with probability q (usually $q = 0.8$). The key variables considered in both versions of the model are the probabilities of prey of a particular level of conspicuousness being either defended or undefended. These probabilities are influenced by the effects of predation over time, and thus we are shown, for example, that conspicuous prey are more likely to be defended than are cryptic prey. Effectively, prey defence levels can evolve, but prey conspicuousness (and thus warning signals *per se*) cannot.

Defended and undefended prey survive predatory attacks with probabilities s_d and s_u , respectively (where $s_d > s_u$). Prey are assumed to live long enough to breed if they survive predators searching 'in their vicinity' on t occasions. Predators are offered prey at random and, assuming that the prey is detected, will choose whether or not to attack, depending on their innate strategy for prey of conspicuousness, p . In the basic model, x_p predators attack prey of conspicuousness p , and y_p predators do not ($x_p + y_p = n$). Predators are rewarded with a fitness benefit b , for attacking an undefended prey item, and receive a fitness deduction c , for attacking a defended prey item (where $c > b$).

Sherratt built an analytic model around the above assumptions and found the evolutionarily stable strategy for predators. Under a range of conditions, the model predicts that all predators should attack cryptic prey on encounter, whereas a mixture of attacking and non-attacking strategies is typically predicted for conspicuous prey. These results are due to the following factors.

- (i) In the model, defended prey are more likely to escape predators, and thus are more likely to survive and reproduce in both cryptic and conspicuous populations.
- (ii) Predators detect more conspicuous prey than cryptic prey, and thus filter out more undefended prey from conspicuous populations. In combination with (i) above, this results in a correlation between prey conspicuousness and defence levels; it is unsurprising that future generations of predators will exploit this information.

In a refinement of the model, an additional strategy was enabled where z_p predators could cautiously attack prey ($z_p + y_p + x_p = n$). This strategy, although resulting in a higher escape probability for both defended and undefended prey (s_{c_d} and s_{c_u} , respectively), brought a lower cost hc to predators for cautiously attacking defended prey. This model was implemented as a computer simulation in which predators were represented as individuals and prey were apparently represented in terms of frequencies. As in the basic model, this model predicts that all predators should attack cryptic prey. However, the refined model predicts that, when encountering conspicuous prey, some predators will not attack at all whereas most will attack cautiously. The resulting predation rates in this refined model are similar, then, to those of the basic model in which roughly half

of the predatory population would attack conspicuous prey. Results in both versions of the model can be interpreted as reflecting the tendency of real predators to 'go slow' on conspicuous prey items (Guilford 1994).

Sherratt uses the model to convey an important point: that the psychological biases of predators may not just be the result of secondary effects of predator nervous systems, but may themselves have been moulded by natural selection. To quote Sherratt (2002, p. 745) '... I question whether defended prey have tended to evolve conspicuousness simply because that happens to have been the type of signal that predators *a priori* find easiest to learn'.

3. METHOD

We now present an individual-based replication of the model described above. The model is extended with a Monte Carlo simulation which calculates the relative survivorships of cryptic and conspicuous prey over a range of parameters; these results may have implications for theories of the two phases of the evolution of warning signals.

(a) *Evolutionary simulation model*

We reworked the analytic model as an individual-based evolutionary simulation, in which predators and prey are represented discretely. The model was built around the same assumptions as Sherratt's model with minor modifications as follows.

- (i) Predators were presented with prey stochastically, with prey items selected using a roulette-wheel selection algorithm acting on prey conspicuousness (i.e. a prey item of conspicuousness 0.9 was nine times more likely to be spotted by a predator than was a prey item of conspicuousness 0.1). This effectively combines the two assumptions of random prey dispersal and higher detectability for conspicuous prey.
- (ii) The order in which predators were presented with prey was randomized after each prey generation to avoid any artefacts that might emerge from a deterministic selection algorithm.
- (iii) Prey randomly reproduced if they were still alive after all n predators finished t foraging attempts (as opposed to surviving if a predator searched in their locality on t occasions).
- (iv) Predator generations lasted an order of magnitude longer than prey generations (generation lengths needed to be explicitly encoded in the model and this seemed a reasonable assumption based on real predator-prey systems).
- (v) The parameter t , representing the number of times a predator encounters prey per prey generation, was increased from 10 in Sherratt's model to 80 in our own (note that t is defined differently in our model), such that a predator will experience 800 predation opportunities during its lifetime.

In line with Sherratt's focus on comparisons between defended and undefended prey within conspicuousness classes, prey population sizes were kept constant at 2000 cryptic prey and 2000 conspicuous prey after each generation. Predator strategies for dealing with conspicuous and cryptic prey were represented as two binary loci, with a one encoding attack and a zero encoding avoidance in each case. Costs and benefits for attacking the different types of prey needed to be explicitly encoded; we used $c = 2$ and $b = 1$ as suggested by Sherratt in an example (other hard-coded parameters, excepting the value t mentioned above, were also set to Sherratt's (2002) example values: see fig. 3 in his paper). The migration rate m , in our model, represents the actual number of migrating prey per generation. Predator fitness was simply the sum of the costs and benefits experienced by an

individual over its lifetime. Successful predator strategies were selected for reproduction using tournament selection (allowing the higher-fitness member of a randomly selected pair of predators to reproduce), and offspring strategies were randomly mutated with a probability of 0.01 per loci.

Each simulation run lasted 1000 prey generations. For each run we recorded the mean frequency of each possible predator strategy over the last 200 prey generations. For each set of parameter values, mean statistics were calculated over 50 runs with different random seed values. In addition to a set of primary runs in which Sherratt's analytic model was duplicated as closely as possible, further runs were performed to systematically vary key parameters, with particular attention to the rate of migration, m . The effects of varying other parameters such as t , c and b were also examined.

(b) *Probability of prey survival*

Before investigating a genuinely coevolutionary model in which prey survivorship is captured explicitly, we wanted to look at how consideration of the question of relative survivorship would affect the results from our individual-based replication of Sherratt's model. Sherratt's model and our replication both give predicted distributions of prey defence levels within a conspicuousness class, and of predation strategies for classes of prey. Given these distributions, a solution to the survivorship question could be found analytically using a hyper-geometric distribution without replacement. However, for simplicity we chose to build a Monte Carlo model. The model took prey defence level distributions and predator strategy distributions from the output of our previous simulation and calculated the mean expected survivorship for conspicuous and cryptic prey over half a million runs. Prey survival was quantified by calculating the percentage of the total population of prey with conspicuousness p surviving each prey season (as in Speed (2001)). The results were then plotted to determine whether or not the tendency of predators to always attack cryptic prey, and to sometimes attack conspicuous prey, actually results in a higher survival probability for conspicuous prey.

(c) *Evolving prey conspicuousness*

Although prey defence levels could be said to evolve in the analytic model, and in our individual-based replication of it, the levels of conspicuousness in the prey population were fixed. To further examine whether we should expect the evolution of warning signals under the set of assumptions explored by Sherratt, we extended our simulation model so that one of the two prey populations could explicitly coevolve its level of conspicuousness: each individual in the simulated prey population carried a gene representing its own value for p . This model allows us to directly address the question of whether a prey population in the model could ever be expected to evolve conspicuous coloration despite the obvious benefits of crypsis. In the simulation one population remains cryptic and the other population starts with a conspicuous coloration; we look at whether the latter population will remain conspicuous over evolutionary time.

In this extended model, mutation could act upon the conspicuousness level, p , of a newborn prey individual with probability 0.01. The effect of mutation was to randomly add or subtract 0.1 from the parental value of p . Minimum and maximum values for p were set at 0.1 and 0.9, respectively. Edge effects in mutation were handled using the reflect operator (Bullock 1999): if $p < 0.1$ then $p = 0.2$ and if $p > 0.9$ then $p = 0.8$. In Sherratt's original model, prey defence levels change owing to the migration of a new prey type. We kept this feature, although it

can be regarded as equivalent to mutation of a gene for a prey's defence level. In our model, migration was therefore implemented by periodically killing a random prey item and replacing it with a new prey item of the same conspicuousness, but with a randomly selected defence level. Predators were equipped with strategies specifying whether or not they would attack prey of each of the nine possible levels of conspicuousness. This 'strategy table' for a predator was inherited and the binary entries in the table could be mutated with a probability of 0.01 per locus. All prey in the evolving population were initially highly conspicuous with $p = 0.9$, and the distribution of prey defence levels was taken from randomly selected final generations in the previous simulation. The evolutionary aspect of the model is used to look at whether warning coloration will be stable over time. Initial strategies for predators were randomly determined. The final mean level of conspicuousness for the prey was recorded over the last 200 generations (of 5000 total generations) across 50 runs.

One way in which Sherratt suggests that his model can successfully predict the evolution of warning signals is by enabling 'runaway coevolution'. Prey migrating into the modelled environment must, of course, come from somewhere else. However, in these alternative locations, they are likely to be under the same kind of selection pressures. Thus, over time, the proportion of undefended conspicuous prey among the total migrant intake will decrease as this unfortunate prey type is filtered out in all possible locations. We have therefore implemented an abstraction of this process in the model. Runaway coevolution was implemented by allowing a separate probability for conspicuous and cryptic populations that a migrating prey item is undefended q_p . If we are to assume that similar predation is occurring outside of the modelled locality, then we can implement this by setting q_p equal to the proportion of undefended prey in the current population each generation. Sherratt suggests that the inclusion of the cautious attack strategy for predators will foster the evolution of warning coloration in general; we therefore enabled this strategy option in our implementation of runaway coevolution.

4. RESULTS

We begin by considering the results of our individual-based replication of Sherratt's analytic model. Figure 1 displays a typical run, and shows the frequency over generational time of predators with attack strategies for cryptic (figure 1*a*) and conspicuous (figure 1*b*) prey in the basic version of the model, in which only attack and no-attack strategies were enabled. Predators evolved to attack cryptic prey but, in the case of conspicuous prey, the population cycled between attack and no-attack strategies.

Figure 2 shows the frequency over time of each predatory strategy for cryptic (figure 2*a*) and conspicuous (figure 2*b*) prey over a typical run, where predators could also evolve to attack cautiously. Predators evolved mainly attack strategies for cryptic prey and cycled between no-attack and cautious-attack for conspicuous prey. Figure 2 shows results that, at first glance, appear somewhat different to the results in Sherratt's fig. 3; however, the basic story is the same. In both cases, predators evolve to a near-universal attack strategy for cryptic prey, and are more cautious about conspicuous prey.

Migration rate was a key parameter in Sherratt's model. Figure 3 shows the mean number of predators with attack strategies for cryptic and conspicuous prey, plotted over a systematic variation of the migration rate. In this case, predators were allowed only attack and no-attack strategies:

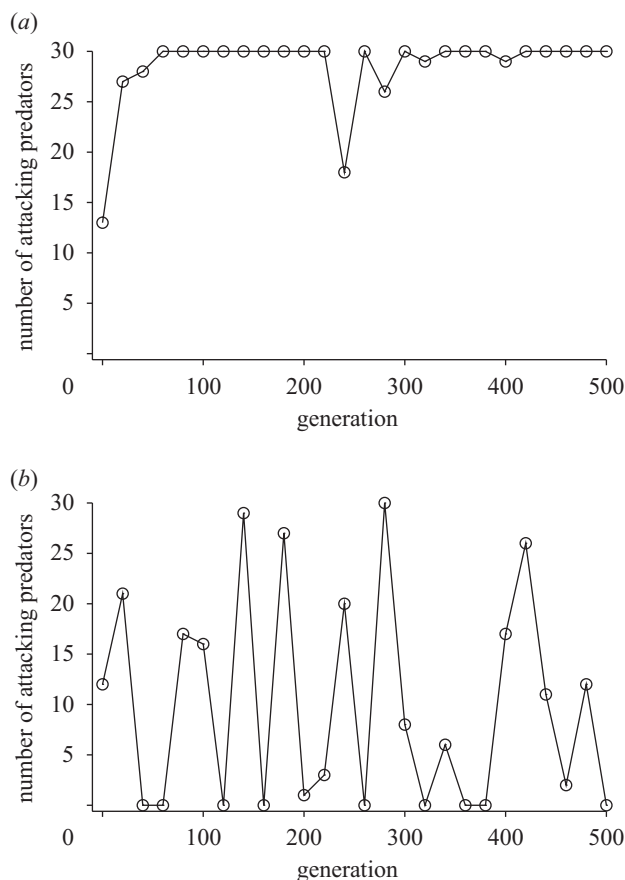


Figure 1. Plot of the number of predators with the attack strategy for (a) cryptic prey, and (b) conspicuous prey, over the first 500 generations of a typical run, where predators were allowed only the no-attack and attack strategies (every twentieth generation plotted). Predators evolve attack strategies for cryptic ($p = 0.1$) prey and cycle between no-attack and attack for conspicuous ($p = 0.9$) prey. In this case $n = 30, t = 80, b = 1, c = 2, q = 0.8, s_u = 0.1, s_d = 0.2$ and $m = 400$.

we find that, over a wide range of migration rates, more predators evolve an attack strategy for cryptic prey than for conspicuous prey. This result shows that Sherratt's finding (that predators are more likely to attack cryptic than conspicuous prey) is robust to variation in the migration rate. When the cautious-attack strategy is enabled (figure 4), predators are still more cautious with conspicuous prey than with cryptic prey under a wide range of migration rates. Similarly, this result is in line with Sherratt's conclusions. Additional sensitivity analyses, not reported here, showed that Sherratt's basic findings were also robust to significant variation, in parameters such as the number of predator sampling events, the costs and benefits of predation, and so forth.

We took the analysis of the simulation further, using a Monte Carlo model to calculate the average differential survivorship across conspicuous and cryptic prey. The results of the Monte Carlo model are shown in figure 5; we find that under a wide range of migration rates, *cryptic* prey are more likely to survive than conspicuous prey. Monte Carlo runs looking at the difference between defended conspicuous and defended cryptic, and undefended

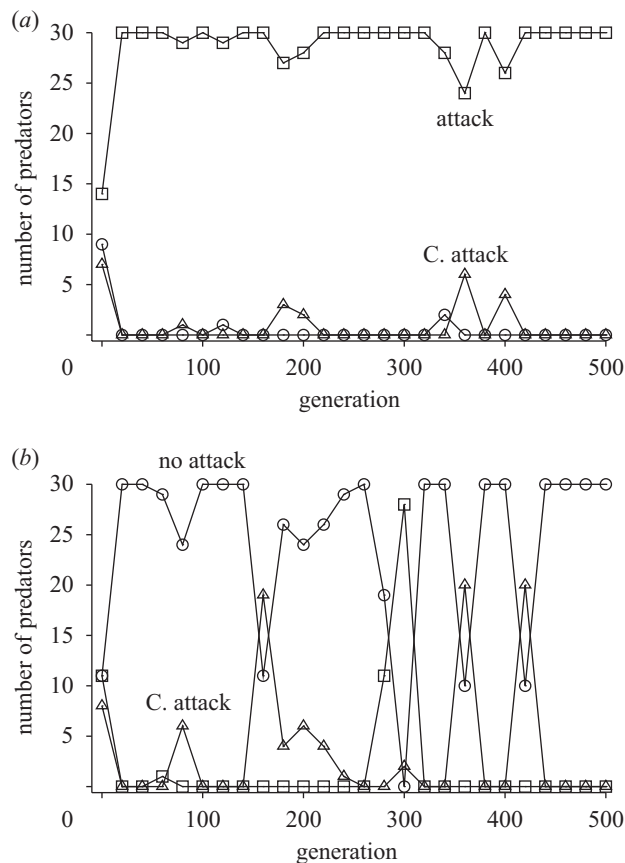


Figure 2. Plot of the number of predators with each strategy for (a) cryptic prey, and (b) conspicuous prey, over the first 500 generations of a typical run, where predators were allowed the cautious attack strategy in addition to the no-attack and attack strategies. Predators evolved attack strategies (squares) for cryptic ($p = 0.1$) prey and typically evolved cautious-attack strategies (triangles) and no-attack strategies (circles) for conspicuous ($p = 0.9$) prey (every twentieth generation plotted). In this case $n = 30, t = 80, b = 1, c = 2, q = 0.8, s_u = 0.1, s_d = 0.2, s_{c_u} = 0.4, s_{c_d} = 0.9, h = 0.5$ and $m = 400$.

conspicuous and undefended cryptic, showed almost identical results: that both defended and undefended prey had a higher survival probability when cryptic. Supporting simulation runs were conducted in which we varied other parameters such as the costs and benefits of predation, and the escape probabilities for defended and undefended prey (graphs not shown). We found that the model consistently resulted in cryptic prey items enjoying higher survival probabilities than conspicuous prey items. Thus, the advantage to conspicuous prey of predators being less likely to attack them is outweighed by the disadvantage of being easily detected.

When we extend the model by giving predators a continuous value representing their attack probability, we find consistent results. Figure 6 shows a typical run where predators evolve a high probability of attacking cryptic prey and a general ambivalence towards conspicuous prey.

Finally, we turn to the results for our explicitly coevolutionary models. When prey conspicuousness, p , is allowed to evolve we find that, under the conditions tested, the prey population always evolves to become highly cryptic, despite the initial population being highly conspicuous (figure 7).

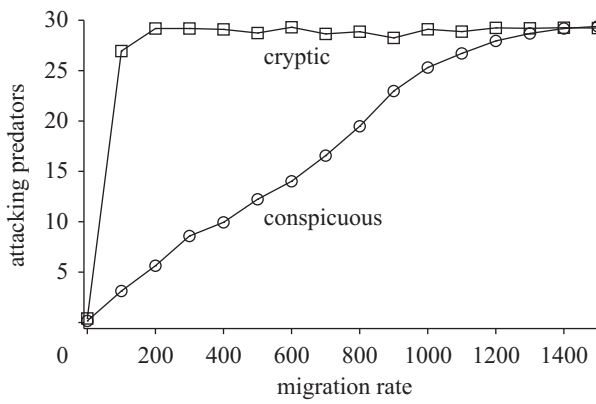


Figure 3. The average number of predators with an attack strategy for highly cryptic ($p = 0.1$) prey (squares) and highly conspicuous ($p = 0.9$) prey (circles), where predators were allowed only the no-attack and attack strategies. Results are plotted against various migration rates and are averaged over the last 200 prey generations of 50 runs. In this case $n = 30$, $t = 80$, $b = 1$, $c = 2$, $s_u = 0.1$, $s_d = 0.2$ and $q = 0.8$.

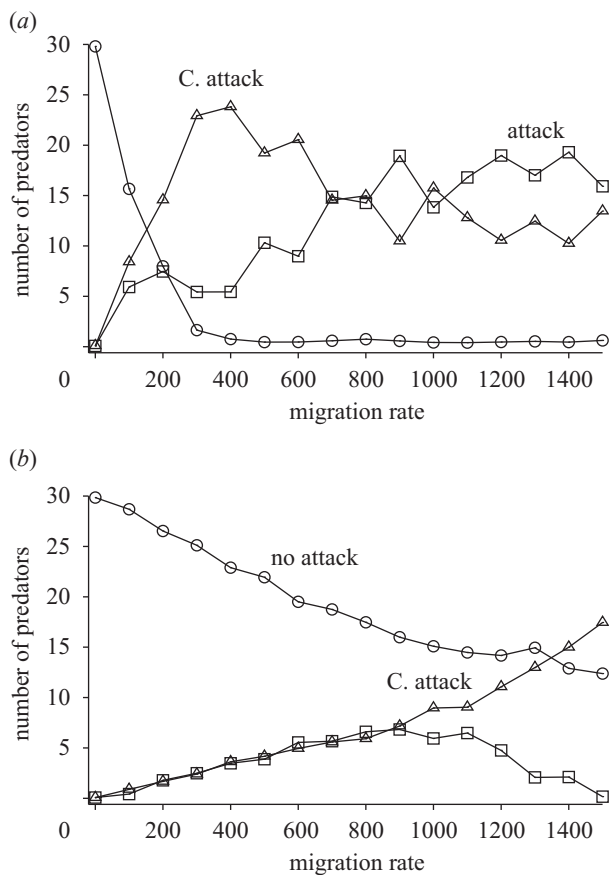


Figure 4. The average number of predators with each type of strategy for (a) highly cryptic ($p = 0.1$) prey, and (b) highly conspicuous ($p = 0.9$) prey, where predators were allowed the cautious attack strategy in addition to the no-attack and attack strategies. Results are plotted against various migration rates and are averaged over the last 200 prey generations of 50 runs. In this case $n = 30$, $t = 80$, $b = 1$, $c = 2$, $s_u = 0.1$, $s_d = 0.2$, $s_{c_u} = 0.4$, $s_{c_d} = 0.9$, $h = 0.5$ and $q = 0.8$.

The results from the Monte Carlo model strongly suggest that evolution will favour crypsis; the results from the coevolutionary model confirm it.

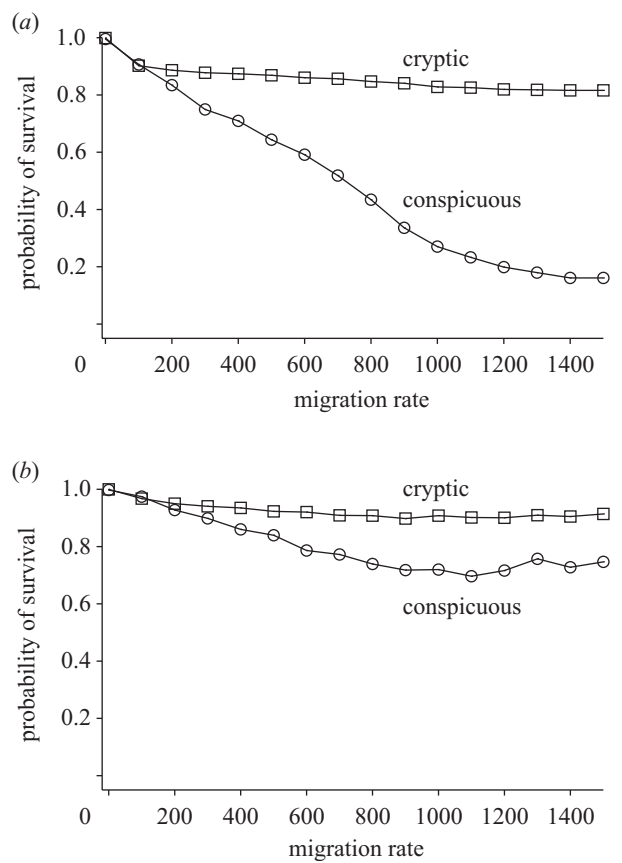


Figure 5. The survival probabilities of cryptic ($p = 0.1$) prey (squares) and conspicuous ($p = 0.9$) prey (circles), plotted against various migration rates. Both when predators had (a) two or (b) three possible strategies, then cryptic prey were typically more likely to survive than conspicuous prey. Results were averaged over half a million runs. In this case $n = 30$, $t = 80$, $b = 1$, $c = 2$, $s_u = 0.1$, $s_d = 0.2$, $s_{c_u} = 0.4$, $s_{c_d} = 0.9$, $h = 0.5$ and $q = 0.8$.

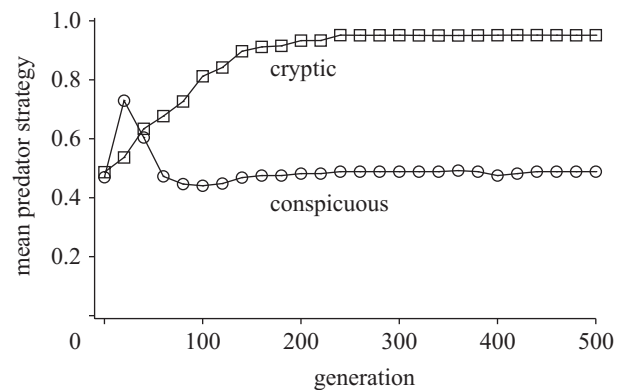


Figure 6. The mean strategy for highly cryptic ($p = 0.1$) prey (squares) and highly conspicuous ($p = 0.9$) prey (circles) in a typical run, where predator strategies were represented as an attack probability in the range $[0,1]$. In this case $n = 30$, $t = 80$, $b = 1$, $c = 2$, $s_u = 0.1$, $s_d = 0.2$, $h = 0.5$ and $q = 0.8$.

When runaway coevolution is enabled (in addition to enabling the cautious attack strategy), we still find that the conspicuous population evolves towards crypsis. Interestingly, the evolving population converges on $p = 0.2$, rather than the minimum conspicuousness level of $p = 0.1$, to distinguish itself from its sister population of

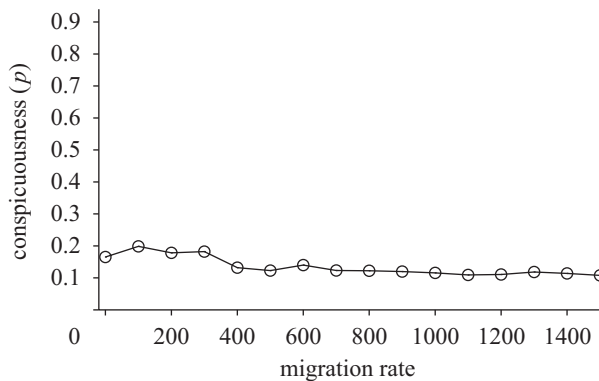


Figure 7. The evolved average conspicuousness of prey plotted against various migration rates. Whether predators had two or, in this example, three possible strategies, prey that were initially conspicuous evolve to become cryptic. Results were averaged over 20 runs. In this case $n = 30$, $t = 80$, $b = 1$, $c = 2$, $s_u = 0.1$, $s_d = 0.2$, $sc_u = 0.4$, $sc_d = 0.9$, $h = 0.5$ and $q = 0.8$.

fixed cryptic prey, which would contain a much higher frequency of undefended individuals (figure 8).

5. DISCUSSION

Our individual-based replication of Sherratt's analytic model confirms that under a wide range of conditions, a general predatory bias to attack cryptic prey more readily than conspicuous prey is predicted. The explanation for this result involves several steps. First, predators filter out more conspicuous prey than cryptic prey, owing to the former type's higher probability of detection. Next, as defended prey have a higher chance of escape than undefended prey, predators act to filter out more undefended prey from the conspicuous population than from the cryptic population. This results in a correlation between conspicuous coloration and high defence levels. Finally, the correlation is exploited by the evolving predators and results in their preference for attacking cryptic prey.

The results of the individual runs shown (figures 1 and 2) generally match those of Sherratt's analytic model. One minor difference is that, whereas the analytic model predicted that roughly half of the predatory population would attack, our model predicts a cycle between all predators attacking and all predators not attacking. Sherratt makes the common assumption that an equilibrium exists in his models (even in his simulation the best predator is copied over the worst). We do not make this assumption and use a tournament selection algorithm. Thus, the cycles are likely to be a result of evolved responses to fluctuations in frequencies of undefended prey and, as is to be expected, some amount of 'sampling error' (although see the continuous version of the model). However, the models give the same predictions on average.

We further scrutinized the simulation by constructing a Monte Carlo model of prey survivorship. The results from this model predict that, under the assumptions and conditions stipulated by Sherratt, cryptic prey will enjoy higher survival rates, and the evolution of warning signals should *not* be expected. Sherratt recognized this limitation for his analytical model, pointing out that the evolved behavioural responses of predators to novel prey cannot in itself explain

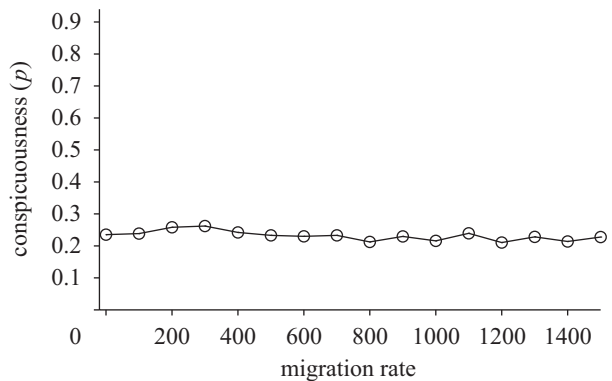


Figure 8. The evolved average conspicuousness of prey plotted against various migration rates. When predators were given three possible strategies and runaway coevolution was enabled, prey that were initially conspicuous evolve to become cryptic. Results were averaged over 20 runs. In this case $n = 30$, $t = 80$, $b = 1$, $c = 2$, $s_u = 0.1$, $s_d = 0.2$, $sc_u = 0.4$, $sc_d = 0.9$, $h = 0.5$ and initially $q = 0.8$.

aposematism, but may help explain why it is not so strongly selected against. This conclusion is further supported by an extended simulation model, in which prey conspicuousness could explicitly evolve. Under the conditions tested, prey always rapidly evolved to be cryptic. Note that we look at relative survivorship across cryptic and conspicuous prey and even though the cryptic population contains a higher frequency of undefended prey than the conspicuous population, we still show that cryptic prey enjoy higher survivorship. This means that conspicuous prey suffer a lower survivorship *despite* having an extra survival advantage in their likelihood of escaping from predators. Thus, this consideration raises an even bigger question mark over why defended prey would ever do anything other than evolve towards crypsis.

Even though our replication of Sherratt's analytic model confirms his predictions, unfortunately the additional analyses we have conducted suggest that his results do not lead to the desired conclusions in an evolutionary sense. The observed predator bias towards attacking cryptic prey does not result in a selective advantage for conspicuous prey once differential survivorship is fully taken into account. This would suggest that theories invoking predator psychology, for example, the need for naive predators to avoid costly mistakes when selecting prey, are still currently the most likely candidates for workable explanations for the fixation of warning signals in a population (Speed (2001) offers a good example of a relevant model). However, it is probable that future models incorporating predator psychology *and* predator-prey coevolution will lead to a more complete picture of the evolution of warning signals.

Sherratt (2002) suggested that, within the framework of his model, one of the most likely scenarios for the evolution of warning signals would be runaway coevolution and the presence of the cautious attack strategy. However, when we explicitly modelled the combination of these two phenomena, we still found that the evolving population tended towards crypsis. The fact that the evolving population clustered around $p = 0.2$ shows that the decision-making process of predators, represented in our model by a simple nine-element strategy, had an effect on the evolution of

prey: the evolving population was caught between a drive for crypsis and a need to remain distinct from the fixed population ($p = 0.1$), which suffered a higher predation rate. Sherratt (2002, p. 745) himself notes that '... learning by direct experience probably plays an extremely important role in facilitating the evolution of aposematism'. Given our results it certainly appears that the psychological properties of predators (generalization, learning, forgetting, and so forth), or other costs to crypsis, may prove vital to our understanding of the evolution and maintenance of warning signals. However, Sherratt's approach, and our additional simulations, suggest that the biases observed in receiver psychology might not be fixed, as is commonly assumed, but may be subject to selection.

Speed & Ruxton (2002) discuss Sherratt's model and suggest that further simulation work is needed to explore the evolution of warning signals under different conditions. Instead of assuming a world that is inhabited by a diversity of defended and undefended prey types; what if we drop the assumption of large amounts of diverse prey migration and assume a world where conspicuous mutants arise only rarely? Our supporting simulation work has shed light on this question. When migration is dropped from the simulation, and occasional prey defence mutation is implemented (in addition to conspicuousness mutating) as with the genuinely coevolutionary model, we find that prey evolve to become cryptic (as in figure 7). Thus, we find that when the assumption of a world inhabited by a highly diverse range of prey types is dropped, prey should also be expected to evolve to become cryptic under the assumptions outlined in the model.

The significant contribution of Sherratt's work is to move theoretical studies of the evolution of warning signals towards considering coevolving populations of predators and prey. This could prove to be a significant advance, as most theoretical studies of warning signals and mimicry consider a lone predator (but see Holmgren & Enquist 1999; Franks & Noble 2004). Although this approach does not explain the survival to fixation of warning signals, it introduces an innovative and promising route to exploring aposematic phenomena.

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