

Batesian mimics influence mimicry ring evolution

Daniel W. Franks* and Jason Noble

Biosystems Group, School of Computing, University of Leeds, Leeds LS2 9JT, UK

Mathematical models of mimicry typically involve artificial prey species with fixed colorations or appearances; this enables a comparison of predation rates to demonstrate the level of protection a mimic might be afforded. Fruitful theoretical results have been produced using this method, but it is also useful to examine the possible evolutionary consequences of mimicry. To that end, we present individual-based evolutionary simulation models where prey colorations are free to evolve. We use the models to examine the effect of Batesian mimics on Müllerian mimics and mimicry rings. Results show that Batesian mimics can potentially incite Müllerian mimicry relationships and encourage mimicry ring convergence.

Keywords: mimicry rings; Batesian mimicry; Müllerian mimicry; evolutionary simulation modelling

1. INTRODUCTION

Mimicry theory dates to a few years after the publication of *The origin of species* (Darwin 1859), and the findings of Bates (1862) were presented as compelling evidence of evolutionary theory (Wallace 1866). However, Turner (1995, p. 131) states that ‘although mimicry is probably one of the most thoroughly explored exemplars [of (co)evolution] it is surprising what we do not know about it’. Mathematical models of mimicry have been useful theoretical tools for examining the costs and benefits to prey as a result of mimicry. They are usually used to examine predation levels on various artificial prey of *fixed* colorations and thus to sketch out the probable evolution of mimetic relationships. However, the coevolutionary dynamics of, and interactions between, different types of mimetic prey have been little explored in models (although see Holmgren & Enquist 1999). Further, it has not been feasible to model mimicry rings (i.e. multi-species mimetic relationships) using such modelling approaches. To address the absence of work on the evolutionary dynamics of mimicry, we present individual-based evolutionary simulation models—in which prey colorations can evolve—to explore the effect of Batesian mimics on Müllerian mimicry relationships and mimicry rings.

2. THEORY

(a) Batesian mimicry

The hoverfly *Chrysotoxum festivum* exhibits a black and yellow striped warning coloration despite being palatable to birds, and lacking a sting. This can be described as a parasitic relationship (see Wickler 1968) as the *model* species, in this case bees or wasps, suffers from a dilution of the aversive effects of its coloration. The mimic, however, gains from the bluff and enjoys reduced predation without the need to evolve a costly defence such as a sting or toxin. This is known as Batesian mimicry (Bates 1862), which can be defined as *a parasitic mimetic relationship between a palatable and a defended species*. In this definition

‘defended’ refers to a natural defence from predators such as a sting or an unpleasant taste.

(b) Müllerian mimicry

Many different *Heliconius* butterflies share a conspicuous coloration, making an honest display as to their anti-predator defences (Mallet & Gilbert 1995). By sharing a coloration, fewer individuals from both species are sacrificed to a naive predator during its learning phase. Thus, both prey species mutually benefit from the relationship. Predators also typically benefit from a reduced educational burden (although see Speed 1993b). This is known as Müllerian mimicry (Müller 1879). This mutualistic mimicry is common among (but not between) many species of butterflies and bumble-bees, and occurs in vertebrates such as poison frogs (Symula *et al.* 2001). Müllerian mimicry can be defined as *a mutualistic mimetic relationship between two or more defended species*.¹

(c) Evolutionary dynamics

Predators generalize over their experiences, owing to predation strategies (Brower *et al.* 1971) or fallible sensory systems. They can therefore mistake approximate mimics for their model. Thus, mimics typically receive more protection as their mimicry becomes more refined (although see Johnstone 2002). Predators can discriminate between prey of sufficiently distinct colorations. For mimicry to evolve, therefore, an initial resemblance (in the eyes of the predator) is needed. This could be arrived at because of various factors such as random drift, large mutations (Turner 1988) or phylogenetic proximity.

The coevolutionary dynamics involved in these forms of mimicry differ (Turner 1987, 1995; see figure 1). Müllerian mimics generally *converge* upon the same colour pattern; selection pressure typically causes both species to evolve ‘towards’ a middle-ground colour pattern.² Batesian mimics *adverge* (Brower & Brower 1972); a conflict of interests between a Batesian mimic and its model results in a coevolutionary arms-race; the mimic ‘chases’ the model through coloration space. The Batesian mimic is typically expected to keep up with the model, as the selection pressure on a Batesian mimic to gain protection is generally greater than the selection pressure on a model to evade the mimic (Nur 1970). Brower & Brower (1972,

* Author for correspondence (dwfranks@comp.leeds.ac.uk).

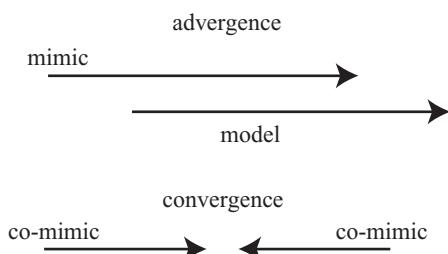


Figure 1. The difference in dynamics between Batesian and Müllerian mimicry. (Adapted from Turner 1995.)



Figure 2. Mimicry ring example. Illustration of three separate species of butterfly that all share the same pattern in a 'yellow' ring. (Adapted from Mallet & Gilbert 1995.) Note similarities and subtle differences in the patterns.

p. 66) state the evolutionary dynamics relevant to this work aptly: '... Batesian mimicry promotes continuous change in time, whereas Müllerian mimicry tends towards stabilization of common colour patterns'.

(d) *Mimicry rings*

Mimicry rings are Müllerian relationships between two or more species. Plowright & Owen (1980) showed that there are five different patterns of bumble-bee in northwest Europe, each constituting a mimicry ring of several species. Another example of a mimicry ring is the tiger pattern shared by different species of *Heliconius* butterfly (Mallet & Gilbert 1995), which coexists alongside other ring patterns (see figure 2). It would presumably be highly profitable for a palatable species to invade these rings as a Batesian mimic, and some such relationships are known to exist. The coexistence of multiple mimicry rings within a geographical region raises a question as to why they do not all converge into a single ring for maximum defence from predators (Turner 1984; Mallet & Gilbert 1995).

3. MATERIAL AND METHODS

Mimicry rings have been little explored theoretically, and have not, to our knowledge, been modelled previously—probably owing to the difficulty that conventional mathematical or stochastic models would have in modelling the large and complex ecosystem required. Evolutionary simulation models, however, are a practical and promising approach to addressing such a task.

When developing simulations, it is useful to first work with a simpler model to which complex features can be added incrementally. Thus, we present an initial model that allows Batesian and Müllerian mimicry to evolve. Thereafter, we present a richer model and examine the effect of Batesian mimics on mimicry ring evolution.

4. A SIMPLE MODEL OF MIMICRY

(a) *Artificial prey*

Multiple populations of prey species were used in each model variation (which we shall refer to as *experiments*). Different species of prey were each assigned a fixed defence level. Each individual had a single gene: a value representing their phenotype or coloration. The colorations were constrained to a 'ring' of values from 1 to 20 (where 20 loops back to 1 and *vice versa*).³ The distance of one coloration from another represented their level of similarity.

(b) *An artificial predator*

A single predator was modelled with a simple reinforcement learning system. The predator's experience of each coloration was represented by an attack probability; after consuming a prey item of a particular external coloration, the attack probability would be updated according to the defence level of the prey item. The predator generalized on the basis of experience and thus would also, to a lesser extent, update its scores for the closest neighbour colorations (see equation (5.1)). The generalization in the simple model was set to a threshold value of 4 (a value chosen to create a landscape of similar, less similar and distinct prey phenotypes). The attack probability gradually degraded back towards ambivalence at a constant rate of 2% per prey generation.

(c) *Model conditions*

For initial simplicity, in each generation the predator was presented with 30 binary forced-choice situations. Two individuals were randomly selected from across all prey populations present and the predator would make a probabilistic attack decision, based on its experience of each coloration. Random reproduction then took place among the surviving prey. Mutation was implemented as a uniform change of ± 1 in the coloration, and the mutation rate was 0.03. All of the experiments were run over 5000 generations, and the populations of prey species were kept constant at 100. The main variable manipulated was the starting distance between prey species' colorations, to determine whether an initial chance resemblance is required for the evolution of mimicry.

(d) *Results*

Figure 3 shows the results of two experiments in terms of the initial and final distances between prey species' colorations. Experiment 1 was conducted using one palatable and one defended species. Regardless of the starting distance between the two, Batesian mimicry evolved: the palatable species came to have the same or very similar coloration as the defended one. This was also true when the function to update the predator's memory did not include generalization.

Experiment 2 was conducted in the same way with two defended species. Figure 3 shows that Müllerian mimicry only evolves if the two prey species have some initial resemblance. If they are initially more than approximately four units away on the phenotypic ring, they typically remain distinct in appearance. Selective pressure dictates that defended species require an initial resemblance to promote a Müllerian relationship.

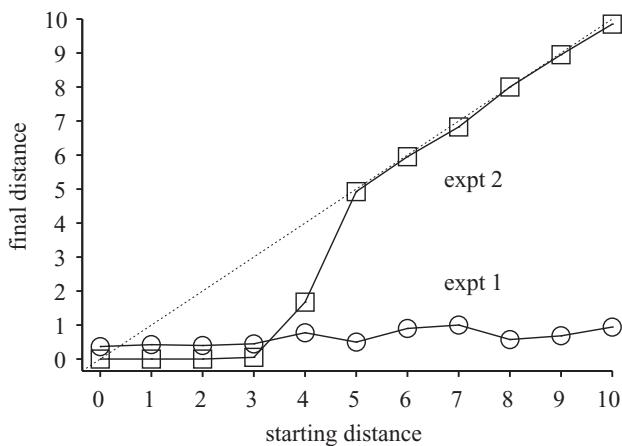


Figure 3. Final distance by initial distance between two prey species' colorations; each point is averaged over 40 runs. The dotted line shows zero change in coloration.

In experiment 3 (no graph shown) simultaneous Müllerian and Batesian mimicry was investigated by including two defended and one palatable species. The results showed that the coloration of the palatable species moved towards that of one of the defended species (i.e. Batesian mimicry). Interestingly, this in turn drove the model species around the phenotypic ring and resulted in Müllerian mimicry with respect to the second defended species, regardless of their initial phenotypic distances (when plotted the results look similar to those of experiment 1).

Further experiments were carried out in which alternative prey were available to the predator. This had no qualitative effect on the results.

(e) Discussion

Experiment 1 shows that Batesian mimics will close in on the model regardless of how different their initial phenotypes are, and regardless of the predator's ability to generalize. This shows that there is more selective pressure for the palatable species to resemble the model than there is for the model to diverge. However, there is an additional reason why the mimic is successful in 'catching' the model: before mimicry has evolved, palatable individuals gain an inherent fitness benefit for mutating away from the average (modal) phenotype of their species. This is because, when presented with a choice, the predator would be more likely to select a well-known phenotype than a newer one.

The results of experiment 2 show that Müllerian mimicry relies on an initial resemblance between the species involved. Such initial resemblance might be caused by any number of factors, such as sexual selection, random drift, phylogenetic similarity and so forth (it should be noted that the *particular* resemblance threshold found in the experiment—in this case four units on the phenotypic ring—is of course determined by the nature of the predator's generalization).

Experiment 3 demonstrates an important finding: that pressure owing to Batesian mimicry can be a force that drives Müllerian mimics together despite a lack of initial resemblance.

5. A MODEL OF MIMICRY RING EVOLUTION

The results in § 4d suggest that Batesian mimics can influence Müllerian mimicry relationships. This implies that Batesian mimics may influence the formation of mimicry rings. In the previous simulation the prey colorations were represented by only a single gene. A richer model will now be presented which incorporates multiple dimensions of prey coloration, and explicitly examines mimicry ring evolution.

(a) Artificial prey

Artificial prey were modelled as populations of individuals with a fixed defence level and a genome representing their coloration. Multiple populations of prey were used in each experiment, and each was assigned a palatability level on a scale between zero and 1 (most to least defended, respectively). The genome consisted of multiple genes with values compositely representing prey coloration; most of the results presented here refer to the two-gene case. The genes were constrained to *continuous* values from 1 to 200 and the Euclidean distance of one coloration from another represented the degree of similarity between phenotypes.

(b) Artificial predators

A population of predatory individuals was modelled with a Monte Carlo reinforcement learning system, as used in a mimicry model by Turner *et al.* (1984). Predators were offered 10 prey per prey generation, which they could either consume or reject. Through experience, the predators could learn to associate prey colorations with a level of defence. As such, they could adapt their probabilities for each coloration as they experienced them, according to the defence level of the consumed prey. The chosen reinforcement learning system of Turner *et al.* was modified to include generalization, to capture the notion that predators will treat similar colorations in a similar way. Predators were modelled as having an attack rating (see equation (5.1)) for each prey coloration. The formula used for generalizing and *updating* these attack ratings after consuming a prey item was

$$P_{t+1} = W(P_t + \alpha(\lambda - P_t)). \quad (5.1)$$

This produces an updated attack rating P_{t+1} , based on the rating at the previous time step (P_t), for colorations at a given similarity distance from the consumed prey whose defence level was λ . The α term denotes a variable learning rate and is calculated using

$$\alpha = 0.5 + |\lambda - 0.5|. \quad (5.2)$$

W is a weighting (used for generalization), which is calculated according to the distance of a coloration from the consumed prey's coloration. If $D > G$ then $W = 0$ (i.e. generalization is finite in extent) otherwise

$$W = \frac{G - D}{G}, \quad (5.3)$$

where G is the predator's generalization rate and D is the Euclidean distance between the coloration and the consumed prey's coloration.

The learning rate is dependent on how far predators' current attack ratings are from the true defence level of

the attacked prey (equations (5.1) and (5.2)). Predators' memories are updated by generalizing over similar colorations within their generalization range, moving outward from the coloration of the attacked prey item (equation (5.3)). This update can be visualized as a cone shape, where the cone tip represents the update for the consumed coloration. The further the coloration is from the one consumed, the less it is updated.

Attack ratings were transformed with the logistic function to give a probability of attack, such that predators were decisive about prey for which they had a relatively strong opinion. Predators made attack decisions by comparing the attack probability to a pseudo-random number in the range of zero to 1. Thus, it was possible for predators to become averse to eating some or even all prey species. We therefore assume that an additional food source is available; predators in the model will not starve even if they refuse all prey items. Predators' memory degraded over time by gradually reverting back towards ambivalence (i.e. an attack probability of 0.5) at a constant rate of 2% per prey offering (as used by Turner *et al.* (1984)). Random asexual reproduction then took place among the surviving prey. After every prey generation the oldest predator would die and be replaced with a new and naive predator.

(c) Model conditions

All of the conditions were run over 200 000 generations and prey populations were kept constant after reproduction. Predator generalization (G) was set to a value of 8 (this value should be considered relative to the abstract phenotypic space, which was 200 units across in each dimension). Stepwise mutation (choosing a random gene to mutate) is commonly used in simulation models, but it has an inherent bias towards orthogonal directions in multi-dimensional genetic space. This could influence the results of the simulation. To overcome this problem a mutation operator was implemented as follows.

- (i) A random direction in the multi-dimensional space was chosen by selecting a random number from a normal distribution (0 mean, unit variance) for each gene.
- (ii) The distance was then selected over a normal distribution (0 mean, unit variance) to allow for varying mutation sizes, with a bias towards smaller ones.
- (iii) The offspring were then mutated in the selected direction at the selected distance.

Note that the mutation operator took place on *every* offspring. The result is that most, but not all, offspring are *slight* variants of their parent with the possibility of rare extreme variants. The issue of mutation bias due to unnatural boundaries (Bullock 1999) was handled using a wrap-around function (making the values 0.0 and 200.0 synonymous) on prey mutations and predator generalization. Attending to such implementation issues is important for avoiding artefactual results in models. They are of particular significance to mimicry models as random drift and mutation are vital to the initiation of mimicry. We consider this type of mutation operator appropriate for this type of simulation, in which there is no distinction between genotype and phenotype, and where the prey representations are additive genetic in character.

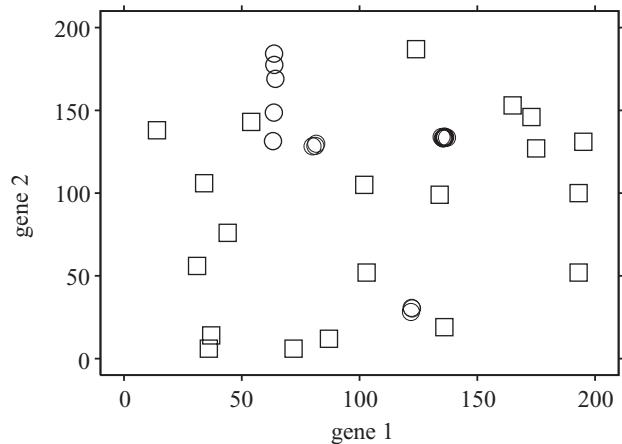


Figure 4. Initial random and final evolved position of each prey species' modal coloration for a typical run with equal population numbers. Squares represent starting colorations and circles represent final colorations.

For our purposes, a mimetic relationship is defined as a Euclidean distance of less than 15 between the modes of two species. The distance of 15 was an approximation calculated by multiplying the generalization rate by 2 and deducting 1 (which gives the minimum distance of overlapping generalization) and then multiplying that by 1.5 (to allow for spread of individuals within a species and generalization over each of them). This gave clusters that matched those found through manual observation of the results.

(d) Experiment

We ran the simulation with various numbers of palatable prey (i.e. potential Batesian mimics). For the results given in § 5f, the prey coloration was represented by two genes. A random initial colour pattern was chosen for each prey species at the start of each run. A defence level of 0.9 and 0.1 was given to defended and palatable prey, respectively. All prey population sizes were kept constant at 300. The simulation results for each experiment were recorded over 20 runs, after which the number of coexisting mimicry rings were tallied.

(e) Sensitivity analysis

The same experiments were also performed with four genes (and an equivalent mutation rate and range of genetic values giving the same sized space of colorations as the two-gene case, using the generalization radius as a reference point). The four-gene results were not significantly different from those presented here. The two-gene results are representative of our findings and are presented here for ease of conveying and visualizing the results. A sensitivity analysis (systematically varying the values of some key parameters) showed that the results are robust. The results of the analysis can be found in electronic Appendix A available on The Royal Society's Publications Web site.

(f) Results

Figure 4 shows the results of a single representative run with no palatable species present. Figure 5 shows the results for a run when four palatable prey species were present. The important points to take from these two figures are that mimicry rings form in both cases (i.e. the

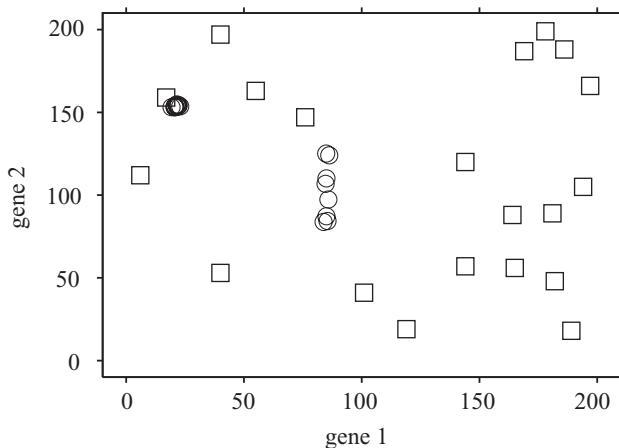


Figure 5. Initial random and final evolved position of each prey's modal coloration for a typical run with four palatable species added. Squares represent starting coloration and circles represent final colorations. Palatable species are not shown; defended species form two large rings and three small rings. Notice how there are fewer rings when palatable species are present.

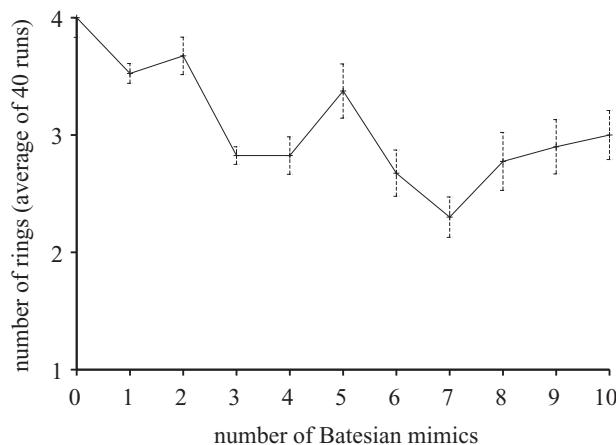


Figure 6. The average number of coexisting mimicry rings formed when a various number of palatable (potential Batesian mimics) prey populations are present

final colorations are clustered) and the number of rings or clusters is smaller in figure 5. The latter result indicates that Batesian mimics have encouraged the formation of a smaller number of large mimicry rings.

Figure 6 shows that as the number of palatable prey species present increases up to three, the number of mimicry rings decreases. Adding more than four palatable species typically results in a number of mimicry rings not significantly different from adding just four palatable species.

A statistical comparison of the number of mimicry rings found in each of the two experiments indicated a significant difference ($t = 5.07, p < 0.001$) with more rings being found with no palatable prey added than with four.

(g) Discussion

When no palatable species were present in the model ecosystem (i.e. there was no possibility of Batesian mimicry) multiple mimicry rings evolved. A further examination of the results showed that in all runs there is little

change from generation 150 000 to 200 000. This long-term stability occurred *despite* the fact that mutation rates were high (every offspring was a mutant) and variation in prey coloration was cost free. If multiple mimicry rings coexist and do not merge into a single ring despite these conditions, we can see that individual rings, once formed, are capable of maintaining their identity in the face of perturbations owing to random drift. The results complement explanations for the diversity of mimicry rings in nature (see Turner 1977; Sheppard *et al.* 1985), which suggests that the colorations of different mimicry rings may be so dissimilar that the rate of major mutations that could allow a species to swap rings tends towards zero.

The results of introducing palatable species show that Batesian mimics can influence the evolutionary convergence of mimicry rings. In the model, palatable species inevitably become Batesian mimics and chase their respective mimicry rings through cycles of colorations, increasing the chance that two mimicry rings might move within convergence range of each other. There is also a threshold over which an increase in the number of palatable species does not *further* reduce the number of mimicry rings. This is because, although Batesian mimics can entice Müllerian relationships, an excess of Batesian mimics can break up or prevent them (Pough *et al.* 1973). We verified this by running the simple simulation with an excess of Batesian mimics. The result was that Müllerian mimicry almost never occurred with respect to two defended species.

6. CONCLUSION

The results of both simulations suggest that Batesian mimics can promote Müllerian relationships and, furthermore, influence mimicry ring evolution. This finding has empirical consequences. If Batesian mimics drive defended species towards Müllerian mimicry, it follows that larger Müllerian mimicry rings should be expected to have a proportionally greater number of Batesian parasites than will smaller rings.

Finally, we would echo a question raised by J. Turner (personal communication). Given that Batesian mimicry occurs so readily in both of the simulations presented, why is it not more common in nature? It seems probable that some factors acting against, or as an alternative to, the formation of Batesian mimicry relationships need to be further studied.

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ENDNOTES

¹Speed (1993a) has also described quasi-Müllerian mimicry. Although this and other exotic forms of mimicry may well be important in nature, for the purpose of this paper we have modelled only classical mimicry relationships.

²Although this is not *always* true; a new immigrant defended prey species might adverge upon abundant existing defended prey.

³The values are in a ring to avoid edge effects (Bullock 1999).

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