

## The Origins of Mimicry Rings

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### Abstract

Mutualistic Müllerian mimicry and parasitic Batesian mimicry can co-exist in *mimicry rings*, i.e., mimetic relationships between multiple species. Theory suggests that all Müllerian mimics in an ecosystem should converge into one large ring. Potentially, the presence of Batesian mimics will encourage convergence. It has been suggested that rare species should seek out common species as models. Mimicry rings have not previously been modelled; we present an evolutionary simulation to investigate the above questions. Complete convergence is not observed although Batesian mimicry is shown to be important factor in the origin of mimicry rings.

Bees and wasps both possess yellow and black striped warning colourations, making an obvious display of their unpleasantness. But why do they display the same pattern? Imagine a situation where they both have different patterns. A predator, such as a bird, would have to sample many of *each* species in order to learn to avoid them both. However, when sharing the same pattern, the predator will see them both as the same type of prey and so will eat fewer individuals before developing an aversion to them. Thus, each individual has less chance of being eaten as it is protected by numbers. It therefore makes sense that two unpalatable (bad-tasting) species would become co-mimics by converging upon the same colour pattern. This is assuming that the predator must learn which prey types to avoid, rather than having innate aversions — an assumption in line with past mimicry research. This type of relationship, in which both species benefit, is known as Müllerian mimicry (Müller 1879).

The honest displays of unpalatability given by species such as bees and wasps are ready targets for free-riders. A good example is the harmless hoverfly, which has black and yellow stripes. It is easy to imagine the benefit gained by a tasty species in being confused for an unpalatable one. So, gaining protection without evolving a costly toxin or sting, the species evolves the same warning colour as an unpalatable species. The species that is being mimicked is termed “the model”. This type of mimicry was the first to be described in the literature and is known as Batesian mimicry (Bates 1862).

Although beneficial to the mimic, Batesian mimicry is detrimental to the survival of the model, as the presence of tasty individuals dilutes the honesty of the warning coloration. This means that Batesian mimicry is a parasitic relationship between mimic and model (see e.g., Wickler, 1968).

Predators have fallible sensory systems and they generalize from their predation experiences. Thus, although they are much more likely to mistake a perfect mimic for its model, they can still mistake approximate resemblances for the real thing. This gives a greater level of protection to a mimic the more accurate its mimicry becomes. However, if the appearances of two prey species are sufficiently distinct, the predator will never mistake one for the other. Therefore, before mimics can undergo a process of pattern refinement, an initial resemblance in the eyes of the predator is needed at first so that it may occasionally confuse the two. An approximate resemblance can be arrived at due to random drift, or fairly large major mutations (Turner 1988).

Population sizes have a considerable effect on mimicry. When two unpalatable species converge as Müllerian mimics, they are doing so in order to increase the population size of individuals with their type of warning coloration. It follows, then, that unpalatable species with higher population sizes are better defended against predators than those with lower population sizes (positive frequency dependence). Conversely, Batesian mimics are better protected by lower population sizes. This is because higher populations would dilute the model’s protection so much as to make predators more willing to risk eating a prey of that colour pattern (negative frequency dependence) (Pilecki & O’Donald 1971).

The coevolutionary dynamics involved in the two separate cases of mimicry differ considerably (Turner 1987; 1995). Müllerian mimics *converge* upon the same colour pattern. That is, they ‘move’ together serving both as co-mimics and models. Batesian mimicry is a different matter. A Batesian mimic’s colour pattern ‘moves’ toward that of the model’s in order to gain protection. The model then attempts to escape the parasitic mimic by evolving its pattern ‘away’ from the invading mimic, as

individuals that are slightly less parasitized (due to minor pattern differences) are more likely to survive. The Batesian mimic is, however, expected to usually keep up in the resulting coevolutionary arms race (Nur 1970). This is because the selection pressure on a tasty species to gain protection is generally greater than the selection pressure on a model to reduce the dilution of predator aversions. This type of mimetic arms race has been termed *advergence* (Brower, Brower, & Collins 1972).

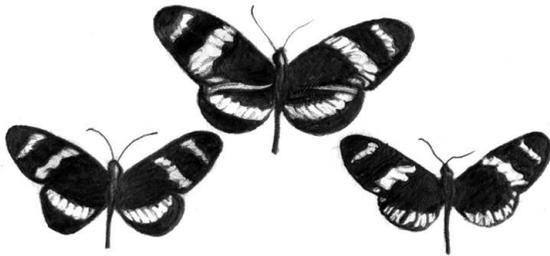


Figure 1: Mimicry ring example. Three separate species of butterfly that all share the same pattern in a ‘yellow’ ring in Sirena. Note the subtle differences in the patterns.

*Mimicry rings* are Müllerian mimetic relationships between two or more species, and are common among butterflies and bumblebees. It is called a “ring” because each species in the relationship has an effect on each of the others. Plowright (1980) showed that there are five different patterns of bumblebee in north-west Europe, each constituting a mimicry ring of several species. A good example of a mimicry ring is the ‘tiger’ pattern shared by different species of *Heliconius* butterflies in Sirena (Mallet & Gilbert 1995), alongside other ring patterns (see, e.g., Figure 1). It would be highly profitable for a palatable species to invade these rings as a Batesian mimic, as it would have less of a dilution affect on the palatability associated with the colour pattern.

The co-existence of mimicry rings in nature has prompted the question: why do the co-mimics (in the same geographical region) not all converge into one large ring (Mallet & Gilbert 1995)? This question is posed because all of the mimics would mutually, and optimally, benefit from evolving into one large ring. The authors have previously shown (Franks & Noble 2002) in a simple, one-dimensional, three-species case that Batesian mimics can ‘chase’ unpalatable species to within convergence range of each other, provoking a Müllerian relationship. This suggests a potential for Batesian mimics to influence the dynamics of mimicry rings.

The above points suggest two working hypotheses:

1. All of the Müllerian mimics in a given ecosystem should eventually converge into one large ring in order to gain maximum protection;
2. If the Müllerian mimics do not converge into one large ring, then the presence of Batesian mimics could entice them to do so, by adverting upon the rings;

Although there are many mathematical and stochastic models of mimicry in the biological literature, this topic has not yet received any attention in the artificial life literature, apart from the authors’ own previous work (Franks & Noble 2002). Mimicry *rings* have hardly been explored at all in any literature, mainly due to the difficulty that a mathematical or stochastic model would have in modeling the large and complex ecosystem that would be required. This is where evolving artificial life models become the most practical and promising approach. To that end, we present a simulation model that explores the evolution of mimicry rings under varying conditions.

### The Simulation Model

To model prey we needed to create populations of ‘agents’ which each have an appearance and palatability level. Multiple populations of prey species were used in each experiment. Different species of prey were each assigned a fixed palatability level on a scale between zero and one (least to most palatable), where 0.5 is neutrally palatable. Each individual had two genes with values compositely representing their external appearance (e.g., a colour pattern) or phenotype.<sup>1</sup> Both genes were constrained to values from 1–200. The Euclidean distance of one phenotype from another represented their level of similarity. Palatable species have values greater than 0.5, and unpalatable species have values lower than 0.5.

A population of abstract predators was modelled with a Monte Carlo reinforcement learning system, as used in a stochastic model by Turner *et. al.* (1984). The predator’s experience of each phenotype was represented by a score of attack probability, which was initialized to ambivalence at 0.5. After eating prey of a particular phenotype, the predator would make a post-attack update of the relevant probability according to the palatability of the individual consumed. The predator would use its experience of different prey appearances to help it decide on whether or not to attack them at the next opportunity. Unlike the stochastic model, the predator generalized on the basis of experience and thus would also, to a lesser extent, update its scores for the closest neighbouring phenotypes accordingly. The formula used for

<sup>1</sup>Clearly a two-dimensional representation of possible phenotypes is a simplification. We have also looked at the evolution of mimicry rings in higher dimensional spaces; similar conclusions are reached but there are significant difficulties in visualizing and conveying the results.

generalizing and updating the probabilities after eating a prey was:

$$P_1 = (P_0 + \alpha(\lambda - P_0)) \times W \quad (1)$$

This produces an updated palatability score  $P_1$ , based on the previous score  $P_0$ , for phenotypes at a given distance from the consumed prey whose palatability was  $\lambda$ .  $\alpha$  is a variable learning rate and is calculated using:

$$\alpha = 0.5 + |\lambda - 0.5| \quad (2)$$

$W$  is a weighting (for generalization) which is calculated according to the distance of the phenotype from the consumed prey’s phenotype, and is calculated with:

$$W = \frac{G - D}{G} \quad (3)$$

Where  $G$  is the predator’s generalization rate and  $D$  is the Euclidean distance between the phenotype and the consumed prey’s phenotype.

The above equations have the effect of updating a predator’s opinion of a particular phenotype. The rate of learning is dependent on how far the predator’s current opinion is from the palatability of the consumed prey (equations 1 and 2). The predator’s memory is updated by generalizing over similar phenotypes within the predator’s generalization range from the consumed prey’s phenotype (equation 3). This update can be imagined as a cone shape, where the tip of the cone is the update for the consumed phenotype. The further away from the consumed phenotype the pattern is, the less it is updated.

Before being used to express the probability of consuming a prey item, scores were transformed with the logistic function, which meant that predators were more decisive about prey for which they had a relatively strong opinion. Predators made decisions about whether or not to eat a prey by comparing the transformed score to a random number in the range of zero to one. This meant that a predator could become averse to eating some or even all of the prey species — note that we must assume that an alternative food source is available as predators in the model will not starve even if they refuse all prey. To implement predator memory degradation over time, each predator’s memory gradually reverted back toward ambivalence (0.5) at a constant rate of two percent per prey offering.

The predator population size was kept constant throughout the experiments at 160. Each predator was presented with 10 potential prey items per prey generation. Prey individuals were randomly selected in proportion to their relative population numbers from across all prey populations. The predator would then make a probabilistic choice of whether or not to eat the prey based on its experience of the phenotype. After being offered a prey item the predator’s memory would degrade,

regardless of its decision. Random asexual reproduction then took place amongst the surviving prey. Every generation the oldest predator would die, and be replaced with a new predator with its memory initialized to the naive attack level of 0.5 representing ambivalence. All of the experiments were run over 200,000 generations and prey populations were kept constant after reproduction.

Mutation was implemented as follows:

1. A random direction in the multidimensional space is chosen by selecting a random number from a normal distribution (0 mean, unit variance) for each gene.<sup>2</sup>
2. The distance is then selected over a normal distribution (0 mean, unit variance) to allow for varying mutation sizes, with a bias towards smaller ones.
3. The offspring then mutates in the selected direction at the selected distance.

Note that the operator is performed on *every* offspring. The result is that most offspring are slight variants or replicas of their parent. This method was used in order to avoid the orthogonal bias present with stepwise mutation operators. Also, the issue of mutation bias due to unnatural boundaries (Bullock 1999) was handled using a wrap-around function (making alleles 1 and 200 neighbours) on prey mutations and predator generalization. These mutation issues are important to any simulation model as they can help to avoid artefactual results. They are, however, of particular significance to mimicry models as random-drift and mutation are vital to the initiation of mimicry.

## Results

For our purposes, a mimicry ring is defined as a mimetic relationship between two or more unpalatable species. A mimetic relationship is defined as a Euclidean distance of less than fifteen between the modes of the two species. The distance of fifteen was calculated by multiplying the generalization rate by two and deducting one (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), which gave clusters that matched that of manual observations for the experiments.

Experiment 1 was conducted with 20 unpalatable prey species. Each had a palatability of 0.1 and population size of 300. After 200,000 generations of evolution, the number of co-existing mimicry rings formed were tallied. Figure 2 shows that five or six mimicry rings usually evolve, and no run resulted in less than four rings. Figure 3 shows the position of the initial modal phenotypes as well as the final coevolved modal phenotypes.

<sup>2</sup>If a uniform distribution was used here, it would give a bias to diagonal directions.

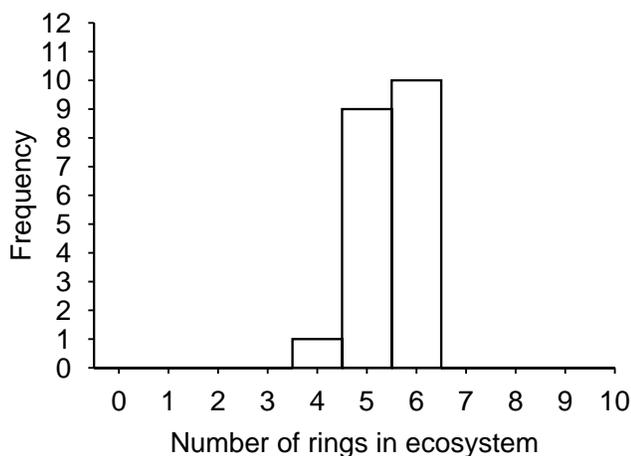


Figure 2: Frequency of mimicry rings after 200,000 generations, with 20 unpalatable species with equal populations of 300 and palatability levels of 0.1. Results were recorded over 20 runs.

Experiment 2 was conducted with the same conditions as experiment 1 except that four palatable species, of population size 300 and palatability 0.9, were also included to allow for Batesian mimetic relationships. Figure 4 shows strong shift toward a lower number of mimicry rings, with four rings being the most common. Figure 5 shows the position of the initial modal phenotypes as well as the final modal phenotypes. Different population sizes were tried for the two experiments, and gave similar results.

A statistical comparison of the number of mimicry rings found in each of the two experiments indicated a significant difference ( $t = 7.333, p < 0.001$ ) with more rings being found in experiment 1 than in experiment 2.

## Discussion

Experiment 1 shows that, under conditions in which all species are (equally) unpalatable, hypothesis 1 was not borne out and thus, at least with the population sizes used, a single large mimicry ring should perhaps not be *expected* in nature. This shows that current mimicry theory explains the co-existence of multiple mimicry rings without the need to bring in other selective forces such as sexual selection. Results show that mimics cluster in rings in different areas of phenotypic space, sometimes far enough apart so that it would be rare for a large enough mutation to bridge the gap. Thus, the phenotypes of the rings are sufficiently different so that the predator would not mistake a member of one for a member of another. Of course, on freak occasions it would be possible for an individual to mutate across the gap. However, it is very unlikely and not guaranteed to be in the right ‘direction’ or beneficial to the individual. Such a state would be well suited to further examination

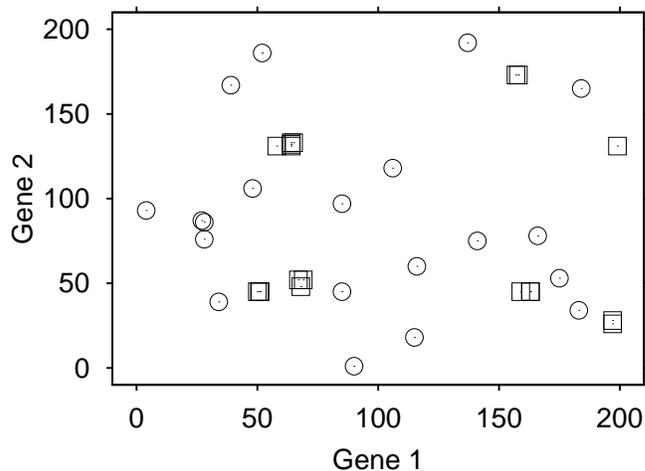


Figure 3: Initial random and final evolved position of each prey species’ modal phenotype for a typical run with equal population numbers. Circles represent starting phenotypes and squares represent end phenotypes. Note the formation of six mimicry rings and one solitary species.

with evolutionary simulation models, as they do not rely finding an equilibrium. A further examination of the results showed that in all runs there is very little (if any) change from generation 150,000 to 200,000, suggesting that the ecosystem has reached a steady state and the various rings are not about to collapse into one large ring given more time. Such an explanation for the diversity of mimicry rings in nature has been suggested in previous mimicry literature (see e.g., Turner, 1977; Sheppard et al., 1985). However, observations of the individual simulation runs shows that the coexisting rings are not *always* far apart. The diversity could perhaps also be explained by the fact that a mutation is unlikely to take an individual from being a perfect mimic of its species’ current ring to being a perfect mimic of another ring; being an imperfect mimic of another ring is not as selectively advantageous as being a perfect mimic of the original ring. Most of the time a mutation will result in an individual no longer being protected by numbers. The simulation shows that current mimicry theory alone does explain the coexistence of multiple mimicry rings.

The results of experiment 2 show that the introduction of palatable species induced a smaller number of mimicry rings, supporting hypothesis 2. This is because, due to pressure to evolve a different phenotype from the modal phenotype of the species (because of negative frequency dependence), the palatable species would inevitably become Batesian mimics. The presence of Batesian mimics would provide positive selection pressure on mutants and would, therefore, increase the probability that they would evolve an initial resemblance to another unpalat-

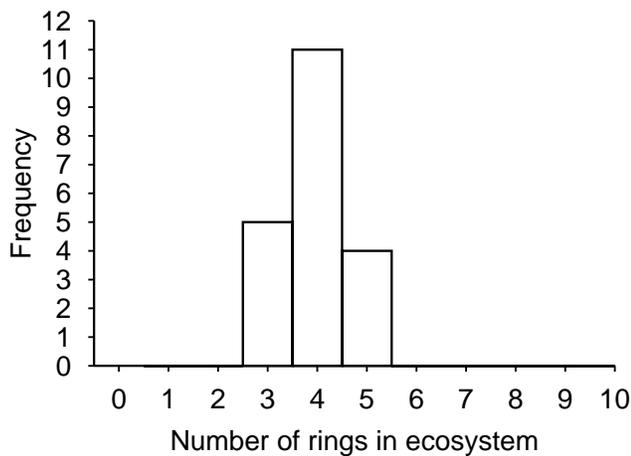


Figure 4: Frequency of mimicry rings after 200,000 generations, with 20 unpalatable species and four palatable species of palatability 0.9 and population size 300 added. Results were recorded over 20 runs. Notice how there are fewer rings when palatable species are present.

able species. Also, Batesian pressure on mimicry rings has the potential to push one ring into the range of another, helping to bridge a large phenotypic difference between them. Once mimicry rings have enough members they can ‘tolerate’ the presence of a Batesian mimic. It appears that situation will persist, unless additional Batesian mimics invade in sufficient numbers to destabilize the ring. As a result, Batesian mimics can induce the convergence of nearby mimicry rings.

Although prey in the model presented had only two genes, work in progress shows that the same conclusions seem to hold for a four-gene case. However, as noted earlier, the two-gene case is easier for display purposes. Future work will endeavour to co-evolve the population of predators with the prey, and to move away from the standard assumption in the mimicry literature that predators learn from a blank slate. This should help to settle any misgivings about the arbitrariness of predator attributes such as generalization distance, learning rate and forgetting rate. Co-evolving predators with prey may also influence the emergence of mimicry rings.

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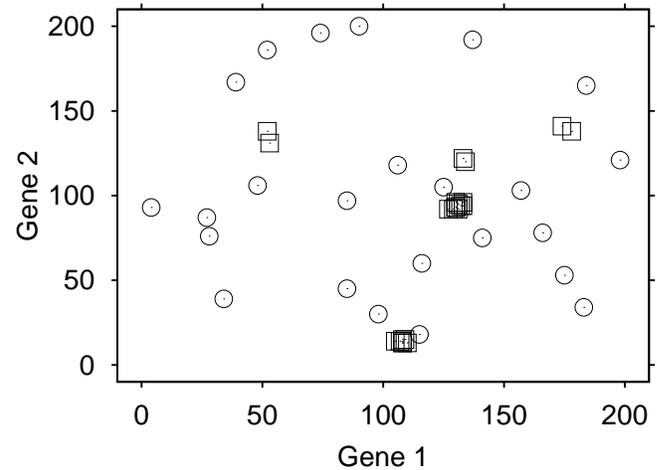


Figure 5: Initial random and final evolved position of each prey’s modal phenotype for a typical run with four palatable species added. Circles represent starting phenotypes and squares represent final phenotypes. Palatable species are not shown; unpalatable species form two large rings and three small rings. Notice how there are fewer rings when palatable species are present.

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