An Agent-Based Model of Mimicry in Coral Snakes

Bachelor's Project Thesis

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Abstract: Coral snakes, a group of American snake species, are characterized by their similar patterns of alternating red, black and sometimes white or yellow stripes. Some of these snakes are harmless, while the bites of others can be lethal. Most research agrees that these coral snakes exhibit a form of mimicry, which is a system in which a species resembles another to gain some evolutionary advantage through deception. The classical example of this is Batesian mimicry, in which mimics (i.e a harmless species) resemble models, the appearance of which is repulsive predators. However, as the predators need to learn this from experience, the lethality of the coral snakes that were thought to be the models has led to research questioning whether this historical view of mimicry applied here. New theories were proposed, and Mertensian mimicry has since been a widely accepted explanation for coral snake mimicry. In that theory, the model-mimic relationship is altered, making the non-lethal but dangerous species the model. This thesis investigates whether Batesian is truly impossible with a lethal model. This is done with an agent-based model, simulating the evolution of a system with a predator, harmless mimic and lethal model. Two systems for the representation of the colour snake pattern are used and compared. The results point to the possibility of the evolution of mimicry with lethal models.

1 Introduction

1.1 Batesian mimicry

Species have evolved many different and fascinating survival strategies over time, such as having adjusted body weight to manage thermal regulation (Bradley & Deavers, 1980), or the ability to shed and regenerate limbs (Arnold, 1984). One such strategy is that of mimicry. First described in detail by Henry Bates, mimicry occurs when one species has similar characteristics to another species, with the effect of deceiving predators (Bates, 1861). This concept was based on the many species of butterflies that seem to 'mimic' the Heliconiinae subfamily. Most Heliconiinae butterflies are inedible, which is advertised by their conspicuous colouration, acting as their primary defence system. These bright colours and even their specific patterns are shared across different species, genera or familiae. Bates describes that, although these butterflies live in similar conditions, their mimicking appearances are unlikely to be a coincidence. There must be an element of deception in mimicry, as the confusion among predators is a key part of the advantage.

1.2 Müllerian mimicry

In Bates's version of mimicry, now known as Batesian mimicry, defenceless species evolve to look like dangerous species. However, as Müller (1878) points out, many of the butterflies described by Bates are actually equally unpalatable and would be regarded as dangerous by predators regardless of mimicry. Müller's paper introduces a new theory in which two species, that are both defended against predators, can be mimetic to share the cost of teaching predators. This has become known as Müllerian mimicry. Müller explains this theory with the first mathematical model of mimicry. This model is explained as such: If a predator species needs to eat 1,200 individuals before learning that this species is unpalatable, and two species consisting of 10,000 and 2,000 individuals respectively lose 1,000 and 200 to that predator species, then they have effectively gained 200 and 1,000 lives due to their mimicry, as both species otherwise would have lost 1,200. In this version, neither species is the model or mimic, as they most likely would have evolved their similar conspicuous colouration in synchrony.

Figure 1.1: São Paulo false coral snake (*Simophis rhinostoma*), found in the Itirapina Ecological Station in São Paulo, Brazil. Image reprinted from Sawaya et al. (2008).

Figure 1.2: Short-tailed coral snake (*Micrurus frontalis*), found in the Itirapina Ecological Station in São Paulo, Brazil. Image reprinted from Sawaya et al. (2008).

1.3   Coral Snakes

A few decades after these foundational forms of mimicry were established, Dunn (1954) coined the so-called "Coral Snake Mimicry Problem". Coral snakes are a group of snakes from different familiae (mainly Colubridae and Elapidae) that show similar colouration and patterns to one another. Their mimicry also shows in other ways, such as how all species of the genus *Micrurus* display similar thrashing behaviours (Moore et al., 2020). Snakes with the coral snake pattern are found in North and South America, and while there are snakes with the coral snake name on other continents, they do not have the same patterns. Species with this colouration possess a wide range of venomosity, with members of the Colubridae family often only having weak venom, while Elapidae are characterized by their large forward grooved hollow teeth, which allow most of them to inject neurotoxins into their enemies (Da Silva & Aird, 2001). Bites from some *Micrurus* snakes are potent enough to kill otherwise healthy adult humans without proper treatment (Bucaretchi et al., 2016). The harmless São Paulo false coral snake (*Simophis rhinostoma*) seen in Figure 1.1 is a mimic of the venomous Short-tailed coral snake (*Micrurus frontalis*) seen in Figure 1.2. These two snakes are from different familiae, yet share the same tricolor triad ringed pattern (Savage & Slowinski, 1992). Predators would not be able to learn to distinguish these snakes in the same way they would be able to learn from but-

terflies, as eating a *S. rhinostoma* would be safe, while they would likely not survive an encounter with *M. frontalis*. Brattstrom (1955) and Hecht and Marien (1956) described the problems of mimicry in coral snakes in detail, listing any reasons why coral snakes look alike and whether they might exhibit a different form of mimicry or none at all. In the second paper, most similarities between pairs or groups of coral snake were labelled as either Batesian or Müllerian mimicry, but not all could be fit into those two categories.

1.4   Mertensian/Emsleyan mimicry

Both papers mentioned at the end of the previous paragraph eventually conclude that while it is a complicated topic, there must be some form of mimicry happening between coral snakes. These papers sparked research searching for specifications about how this form of mimicry would work. Mertens (1956) contains a detailed explanation of all potential factors for the coral snake pattern, and lays the foundation for a new theory of mimicry. Bites from snakes of the *Micrurus* genus, which had always been seen as the model species, are fatal to almost all their predators. Since the predators cannot learn from their experience after death, Mertens suggests the *Micrurus* snakes to be the mimics, while non-lethal venomous snakes are the models. Predators would learn their aversion to the pattern from their experiences to the repul-

sive but non-deadly coral snakes. This is the basis of the form of mimicry usually associated with coral snakes. Wickler (1968) describes this form in more detail, and coins it Mertensian mimicry. Pasteur (1982) has included it in his review of mimicry systems as the explanation for the "Coral Snake Mimicry Problem", calling it Emsleyan mimicry instead, attributing the discovery to Emsley (1966), who came up with and formally described the details of the system like Mertens and Wickler did.

1.5 Other explanations

Most research on coral snakes over the years has accepted a view of Batesian or Mertensian mimicry (Greene & McDiarmid, 1981; Thomas et al., 2022). However, some researchers believe there might be another explanation. In recent literature, Loeffler-Henry and Sherratt (2021) suggested that coral snakes might not benefit from predator avoidance, but rather inappropriate attack strategies from the predators, such as carelessness when expecting a harmless prey. However, research has shown that predators do avoid the coral snake pattern. Studies done in Costa Rica (Brodie, 1993) and Argentina (Buasso et al., 2006) show that plastic replicas of snakes with the coral snake pattern are attacked significantly less often than replicas with other patterns. Some research suggests predators learn this avoidance through empathetic learning (Pough, 1988): predators might see others experience the consequences of eating coral snakes and learn from this. Still, this has been said to be unlikely as most coral snake predators do not hunt in groups. Another theory is that the avoidance of these snakes is innate. S. M. Smith (1975, 1977) showed two species of bird which do not have heavy protective scutes on their legs hesitate to attack ring patterned models when they resemble coral snakes, even when taken away from their nests at a young age. She also showed that these birds have a generalized aversion for different kinds of coral snake patterns. This would suggest the predators have learned to avoid a certain pattern over generations, giving predators that have this innate avoidance an evolutionary advantage over those that do not. Species that have not evolved to avoid coral snakes (DuVal et al., 2006; N. G. Smith, 1969) have developed other strategies or defences to protect themselves against snake bites.

1.6 The aim of this paper

This text aims to investigate the details of mimicry in coral snakes. An assumption is made that coral snake mimicry follows rules similar to that of Batesian mimicry, wherein the more dangerous, and in this case lethal, species is the model, while the less dangerous species is the mimic. It is also assumed that predator learning happens over generations, similar to the adaptation of the colouration by the mimics. What this text hopes to show is that other explanations such as Mertensian mimicry are not necessary to explain the Coral Snake Mimicry Problem, instead fitting as a form of Batesian mimicry with evolutionary learning. The question asked here is whether the assumption of lethal models would allow for the evolution of (Batesian) mimicry.

1.7 Computer modelling

Investigating whether Batesian mimicry is possible with lethal models through evolutionary learning would be difficult with field work alone. Müller's mathematical model of mimicry shows that models can be used to simplify situations to gain an understanding. More complex models can also simulate and create the necessary data for analysis that would be too hard to obtain otherwise. Instead of investigating data from the real world environment, a model of said environment can be made based on assumptions about it. Reddingius (1970) notes that "models used for theoretical purposes need not always be very general or realistic, as long as they are suitable for making a point." His article describes the ways in which models might be used, and highlights the use of models in demonstrating a theory or proving one wrong. All details are known about a model, in contrast to the real world. When comparing the data from the model to what is expected from real world experience, claims can be made about which parts of the model are fair explanations, and which parts do not line up.

1.8 Models of mimicry

An example of a model created for the coral snake mimicry problem is by Franks (2005). He analyses an individual-based evolutionary simulation model to investigate various aspects of mimicry. His focus

lies on the evolution of Müllerian mimicry rings, which is when multiple unpalatable species all resemble each other, and how Batesian mimics then influence such rings. It is claimed that the model presented is the first of its kind, as it allows for both mimicry and conspicuousness. This same thesis also showed warning signals are able to evolve after mimicry has already occurred, which is presented as one of the explanations for the coral snake mimicry problem. Additionally, it shows that model species are able to evolve more warning signals to distinguish themselves from mimics. There is not yet a model that investigates the influence of lethal model species on mimicry systems.

1.9 Agent-based modelling

Agent-based modelling (ABM) is a type of computer modelling. When ABM is referred to with a determiner (e.g. an ABM) or as plural (ABMs), it stands for agent-based model instead. A book by Wilensky and Rand (2015) is a thorough guide for the usage of these kinds of models. They describe ABM as being "constructed out of individual objects and simple rules for their movement of behaviour" and therefore easier to understand than other models, such as mathematical ones. In chapter 0, "Why Agent-Based Modeling?", Wilensky and Rand describe how even with simple rules, ABM allows for easy analysis of any emergent patterns or interesting interactions between the agents involved in the model. One of the authors of this book is also the author and developer of the multi-agent programmable modelling environment NetLogo (Wilensky, 1999).

1.10 Mimicry in NetLogo

NetLogo has a library of example models. One of these is one on mimicry, simulating the Batesian relationship in which viceroy moths (*Limenitis archippus*) mimic monarch butterflies (*Danaus plexippus*) (Wilensky, 1997). This relationship has been another well documented example of mimicry since Van Zandt Brower (1958) showed birds learn to recognize the monarchs as inedible, after which they refused to eat the identical looking viceroy moths as well. Although the specifics of the relation between monarch and viceroy have been called into question (Ritland & Brower, 1991), the ABM

remains valid as an analytical tool for Batesian mimicry in general, showing how a palatable species could evolve to look identical to an unpalatable one. The ABM consists of three species of agents: models, mimics and predators. Predators eat the models and the mimics, although they do not need to eat to survive. Predators remember the colour of models they eat and refuse to eat that colour. The predators can learn up to three colours at a time and the prey agents have ten colours they can be. Models and mimics are able to asexually reproduce and their children have a small chance to become any one of the other nine colours. When this model is run, it reliably shows the mimics evolving towards the same colour as the models, after which they retain that colour, as they no longer get eaten.

2 Model description

This section explains the agent-based model (ABM) used to investigate whether mimicry can evolve when the models are lethal. The ABM is created in NetLogo version 6.4.0. As described before, their models library contains a model on mimicry (Wilensky, 1997). This model has acted as an initial place of inspiration, but the implementation presented in this paper is original.

NetLogo measures time in discrete time steps called ticks. These are a standardized measure of time as opposed to seconds which would depend on the processing speed of the computer the model runs on. The code decides when the next tick starts.

2.1 Model Summary

Like Wilensky's ABM, there are three species of agents: models, mimics, and predators. Models and mimics will be collectively referred to as prey agents. Each species is able to asexually reproduce unless its carrying capacity is reached. The number of agents for any one species cannot exceed its carrying capacity. When the simulation is set up, the maximum number of agents for each species is spread out randomly across the world. Each species has one inheritable trait, prey agents inherit their colour and predators inherit a preying colour. This preying colour is the colour they recognise as edible prey. Instead of avoiding, for example, agents with the coral snake phenotype, they will have a
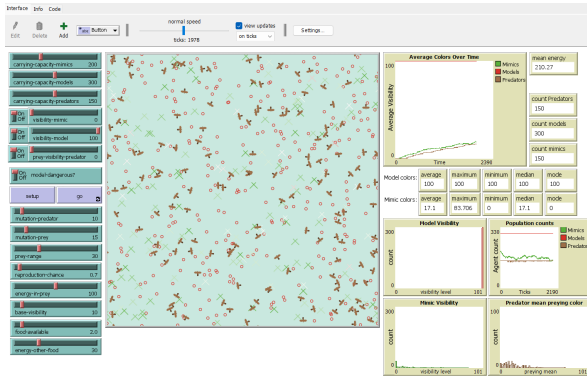
Figure 2.1: The ABM's NetLogo environment.

certain idea of what an edible agent would look like. This is in line with how the plastic replicas would be attacked as long as they somewhat resembled edible snakes (Brodie, 1993; Buasso et al., 2006). Models start with bright warning (aposematic) colours, while the mimics are camouflaged at the start. The predators start by recognising the colouration of the mimics as edible, avoiding anything else. The world is made up of 100 by 100 square tiles. The agents are not restricted by these tiles in their movement, as they can move in any direction, but a predator can only see its prey when they are on the same tile. When an agent reaches one of the edges of the world, they will be moved to the opposite edge, effectively wrapping the world into a torus shape. This is done so the agents are not caged by their environment, eliminating this as a confounding variable. The NetLogo environment can be seen in Figure 2.1.

The colours of the prey agents are an important part of this ABM. A representation of the possible colours and their associated values can be seen in Figure 2.2. The colours represent the visibility value of a prey agent, which runs from values of zero to one hundred. Together with a global base visibility that is set by one of the sliders, this value is the chance a predator spots that prey item once they are close enough to each other. Without the base visibility, prey with a visibility level of zero would be invincible. High visibility level values represent aposematic colouration, while low values represent camouflage or cryptic colouration. The inheritable trait of the predators also uses this same 0-100 scale. This value represents their preying mean,
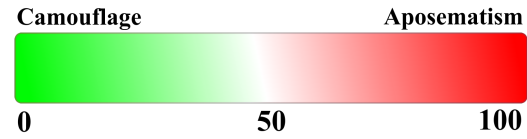

Figure 2.2: Colours and their associated visibility levels in the linear colour system.

which is the colour or visibility level of prey they recognise as edible. A global variable, `prey-range`, determines how far away from this mean they are willing to accept as prey. More about this is explained in Section 2.4.

Predators also have an energy level. This starts at a value of 200, but decreases by one each tick. If it reaches zero, the agent dies. Eating a prey agent can increase their energy level, the amount of which is set by a parameter with the sliders. However, since models are lethal, eating a prey agent of the model type will kill the predator along with its prey. These two ways the predators can die combine to make their evolutionary force. They need to eat prey agents, but also need to avoid models. Finally, each tick, every predator has a certain chance to gain a small amount of energy. This chance and the amount of energy can be set with the sliders. It exists to keep the predators from dying out too easily, simulating other food sources.

2.2 Alternative colour system

Besides the linear colour system seen in Figure 2.2, an alternate colour system will also be explored, taking inspiration from the implementation of a circular colour system in the thesis by Franks (2005), who explains how this system avoids potential edge effects. In the linear system, agents close to the extreme values of 0 and 100 can only evolve towards the middle. This could cause mimicry to be easily indistinguishable from a situation in which both prey species simply experience the same evolutionary pressure to avoid predators. For examples, models and mimics might get stuck at high visibility values, unable to evolve into lower values, if those lower values are where the predators would recognise them as edible.

A representation of the circular system can be seen in Figure 2.3. The visibility value now has a range of −100 to 100, where those extremes repre-
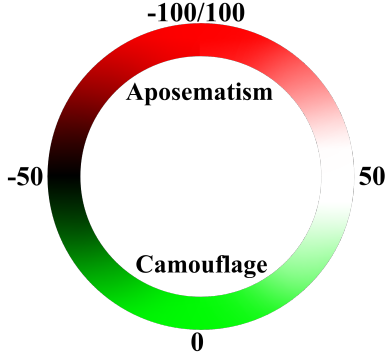
Figure 2.3: Colours and their associated visibility levels in the circular colour system.

sent the same point. To differentiate between negative and positive values in the visual world interface, negative values go through black instead of white. For visibility purposes, there is no difference between negative and positive values, as they represent the same chance to be spotted. However, the predators are able to distinguish these two sides when deciding whether or not they deem a prey agent as edible or not.

2.3 Agent behaviour

At the start of each tick, all agents 'wiggle'. This means moving in a random direction by first rotating a random number of degrees below 100 to the right, doing the same to the left and then moving forward the length of one tile. This value of 100 is carried over from Wilensky's ABM. Then, if possible, the predators select a random prey agent on the same tile as them. Before the selected prey agent is attacked by the predator, it needs to first be spotted and then recognised as edible prey. Equation 2.1 describes the probability of a prey agent being spotted and is based on the (absolute) visibility level of the model/mimic (V_m) and the global variable `base-visibility` (B), which can be set with one of the sliders. The `base-visibility` plus the visibility of the prey agent represents the exact chance that agent has to be seen by the predators. This could lead to values above 100, in which case the prey agent is just always spotted by predators, as if it had a value of 100.

$$P(\text{p sees m}) = \frac{|V_m| + B}{100} \qquad (2.1)$$

The probability of a predator wanting to attack the selected prey is based on the predators' `prey-range` (R) and the difference between the colour of the prey agent (V_m) and the visibility value the predator recognizes as edible (V_p). If this distance is more than the `prey-range`, the predator does not attack. When there is no difference between the prey agent's V_m and and the predator's V_p, there is a 100% chance the predator will attack the prey agent. When this difference is as big as the prey range, this chance becomes 0%. If the difference is bigger than the prey range, resulting in a negative number, prey will also not be attacked. This range of potential edible prey is based off the way predators in the studies by Brodie (1993), Buasso et al. (2006), and S. M. Smith (1975, 1977) seemed to attack replicas based on their similarity to their regular prey.

$$P(\text{p attacks m}) = \frac{R - |V_m - V_p|}{R} \qquad (2.2)$$

When a predator has selected its prey, it first checks if it can spot the prey agent (Equation 2.1). Only if this has returned true does the predator attempt to recognise the prey as edible (Equation 2.2). If a predator, based on those two probabilities, attacks the prey it has selected, one of two things can happen. If the selected prey is a model, both predator and prey die. If the selected prey is a mimic, only the mimic dies, and the predator gains energy, the amount of which is set by the `energy-in-prey` slider. After the attacking stage, predators have a chance to gain energy from alternative food sources. This chance is decided by the `food-available` slider, and the amount of energy gained each time by `energy-other-food`.

Finally, all agents have a chance to asexually reproduce if their species' carrying capacity has not yet been reached. When a new agent is born, they are mostly identical to their parent, except for their colour if they are a prey agent or their preying mean if they are a predator. This is chosen from a normal distribution where the mean is their parent's colour and the standard deviation is a variable set by the sliders. When the new colour falls outside of the colour system, this value will 'bounce back'. For example, if a new agent should receive visibility level 103, it will instead be born with a value of 97.

Variable	Value	Explanation
`carrying-capacity-mimics`	200	Maximum amount of mimics that can exist in the environment at any given tick. Mimic agents are only able to reproduce below this limit.
`carrying-capacity-models`	300	Maximum amount of models that can exist in the environment at any given tick. Model agents are only able to reproduce below this limit.
`carrying-capacity-predators`	150	Maximum amount of predators that can exist in the environment at any given tick. Predator agents are only able to reproduce when below this limit.
`mimic-set-visibility?`	True	Boolean of whether the visibility of the mimics is a set value. If set to False, all mimics will start with random visibility values.
`visibility-mimic`	0	Starting visibility of all mimics, if set. (Camouflage)
`model-set-visibility?`	True	Boolean of whether the visibility of the models is a set value. If set to False, all models will start with random visibility values.
`visibility-model`	100	Starting visibility of all models, if set. (Aposematism)
`predator-set-visibility?`	True	Boolean of whether the visibility of the predators is a set value. If set to False, all predators will start with random preying means.
`prey-visibility-predators`	0	Starting value of the visibility level all predators recognise as edible prey if set.
`model-dangerous`	True	Boolean of whether eating a model will kill a predator.
`mutation-predator`	10	Standard deviation used when deciding which value the inherited preying preference will be after reproduction.
`mutation-prey`	15	Standard deviation used when deciding which value the inherited visibility level will be after reproduction.
`prey-range`	30	Predator's range outside of which they cannot recognise a prey agent as edible. Represented by R in Equation 2.2.
`reproduction-chance`	0.7%	Chance of any agent to reproduce.
`energy-in-prey`	100	Energy gained from successfully eating a mimic.
`base-visibility`	10	Base visibility of any prey. When they have a visibility level of 0, they will have a chance of `base-visibility`% of being seen. Represented by B in Equation 2.1.
`food-available`	2%	The chance of predators finding an alternative source of energy during a tick.
`energy-other-food`	30	Energy gained from eating an alternative food source.

Table 2.1: **All variables of the model with their default values. The value shown in the second column is the default valued used in every run shown in the results section, unless when specified otherwise. These values were chosen during testing as they produced promising results or seemed realistic.**
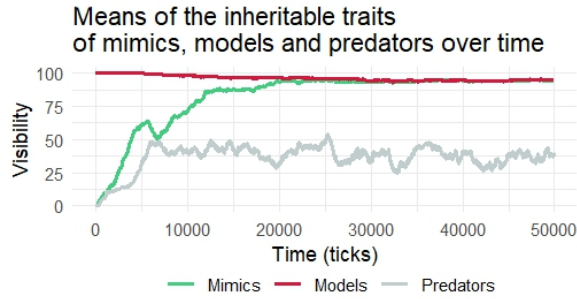
Figure 3.1: Means of the inheritable traits of all three species over the course of 50,000 ticks. Settings are as described in sections 2.1 and 2.4.
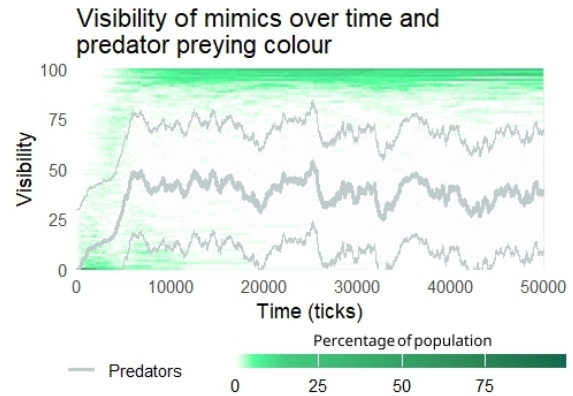

Figure 3.2: Alternative graph of the data displayed in Figure 3.1. The models are left out and the mimics are represented by a heat map. Darker greens signify more mimics having that visibility level during that tick. The mean of the predators now also displays the prey-range that a predator with this value would have.

2.4 Chosen variables

The ABM uses global variables which can be set with the sliders and switches in the NetLogo interface panel seen in Figure 2.1. Table 2.1 explains all variables used in the model. Most of the variables do not need to be these exact values, and can often be changed while still producing similar results.

2.5 Data collection

From testing the ABM during development, it was found that interesting results would usually emerge around or after 25,000 ticks. To analyse the evolution of the agents, the simulation will be run for 50,000 ticks. From these runs, the visibility levels of all prey agents and the preying means of the predators will be recorded to analyse their change over time. To be able to conclude mimicry is possible, the colours of the mimics should resemble those of the models, with clear indication of the mimics benefitting from the learned avoidance of the models. Since there is no way to quantify the resemblance to mimicry, a single run will be displayed or described, which will be representative of a typical run with those settings unless otherwise stated.

3 Results

Since the predators work with the same 0–100 scale as the models and mimics, the term "visibility level" will be used for all three species. This refers to the actual visibility level, or the colour, of the prey agents, while for the predator agents it refers to the visibility level they recognise as edible prey.

3.1 Linear colour system

Figure 3.1 shows the evolution of the visibility levels of the three species with the linear colour system setup as described in the previous section. The mimics immediately evolve away from the predators. Since they start at the lower end of the linear colour system, they can only evolve higher values, towards the mimics. The predators follow the mimics, also evolving to higher values. However, they stop after about 6,000 ticks, around a mean value of 50. At the start of the simulation, the predators eat a lot of the mimics, causing their energy values to skyrocket. These predators are able to survive for a long time without eating more mimics, keeping the predator mean low. Most predators also do not evolve much further than 70, as ones with higher values often die from consuming models. Mimics continue evolving to higher values, and after about 20,000 ticks the mimics are nearly indistinguishable from the models.

There is a drop in the mean value for the mimics around 6,000 ticks. This commonly happens in runs with this setup. Figure 3.2 shows more context for this. In this graph, the visibility levels of the entire mimic population are shown in green, along with an overlay of the mean of the predators and the preying range that predators on that mean would have

in grey. In the first few ticks, the entire mimic population is in the lower left corner. As time moves on, the mimics evolve higher values as they get eaten by the predators, whose preferred preying colour evolves to higher visibility values as well. Once the predators have evolved to have preferences above 30, and mimics with a low visibility are no longer eaten by predators, those who survived at low visibility levels are able to reproduce quickly enough to bring the average visibility of the mimics down for a few thousand ticks. After a little while, predators return to eat the mimics with low visibility values, bringing the mean visibility up again.

3.1.1 Random starting values

These kinds of jumps, where the mean value of the mimic temporarily moves back towards camouflage, happen more often if the ratio of mimics to predators is higher. They happen less frequently if the starting visibility levels of the mimics and predators are set to random values. However, even with these alternative setups, the mimics still evolve to have a visibility level similar to the models. In a setup with random starting values for models and mimics, the predators at high values quickly die out, creating a "safe space". Mimics initially are safer with camouflage, but quickly evolve to higher values once this safe space has been established and these higher values are no longer considered edible by predators. An example of this can be seen in the first 10,000 ticks of Figure 3.3. Models are preyed upon more in this setting as there are predators who start with high values, so their eventual mean is lower compared to a run with set starting points for all agents. Whether the starting point for predators and mimics is 0 or random, the mimics usually get to the same visibility level as the models around the same point, about 20,000 ticks.

3.1.2 Model to mimic ratio

Even when there are far more mimics than there are models, mimicry seems to occur. This would go against the idea that Batesian mimicry requires there to be more models than mimics. Figure 3.3 shows a run with mimics far outnumbering the models. We can see the mimics initially evolve towards camouflage (i.e. lower colour values), as explained in the previous section, but quickly move
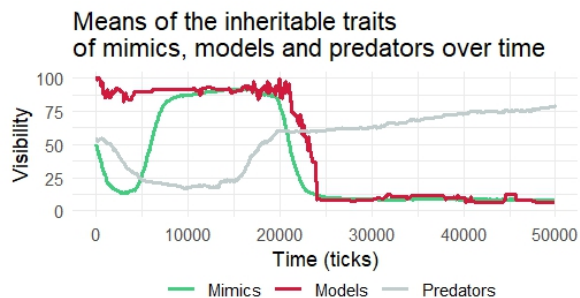

Figure 3.3: Run with 10 models, 600 mimics, and 150 predators. Mimics and predators start with random values for their inheritable traits, while models start at 100.

towards the models once that is safe. After a while, predators are no longer able to survive without eating mimics, resulting in an evolutionary pressure to evolve higher preference values. Since there are so few models, their mean can easily shift to other values, causing both prey agents types to eventually evolve to lower values after 20,000 ticks. This does require the models to reproduce fast enough to keep up their population numbers immediately after death, and is thus dependent on unrealistically high reproductive rates.

3.1.3 Camouflaged mimicry

This convergence between models and mimics at high visibility values happens in many simulations. However, there are a few combinations of variables in which the opposite occurs. For example, of 100 runs where all three species start with completely random values, both prey agents types evolve towards low visibility levels 47 times. When the starting values are completely random, the predators should have more encounters with models with high visibility levels as they are more likely to be detected and eaten. This means both models with high visibility and predators with high preference values die more often, which which is why both models and predators are driven away from these high visibility levels initially. Depending on whether models or predators with these high values go extinct first, which happens randomly each time, this either results in a "safe space" for predators to evade models or one for high visibility prey animals to evade predation.
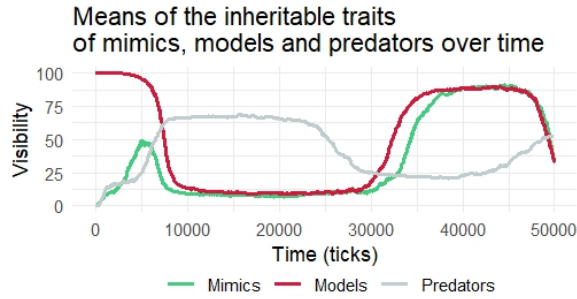
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Figure 3.4: Typical run with harmless models, meaning predators can only die from starvation. Models and mimics evolve towards camouflage until they are eventually driven away by predators with low visibility preferences. Models and mimics look alike, but this does not provide the agents with any advantage.

3.1.4 Non-lethal models

When the models are not dangerous, so when there is no difference between the two prey species and the predators can only die of starvation, prey agents always experience an evolutionary pressure towards low visibility levels. Figure 3.4 shows an example of such a run. The mimics initially evolve towards higher values, similar to the run with dangerous models. The predators mostly follow, evolving towards a mean value of 60, some preying on models, some on mimics. Once the models start being preyed upon, they quickly evolve towards lower visibility values to benefit from the camouflage. Since the predators gain a massive energy boost from eating prey at the start, and receive additional energy on top of that, barely any agents die and evolution slows down as the carrying capacity prevents new agents from being created. The situation in which both models and mimics are camouflaged while predators are too far away to recognise any prey agents as edible, remains for nearly 20,000 ticks. After some time, the predators have lost their initial stored energy and start evolving towards the prey agents. When the mean preying colour has gone down enough, around 28,000 ticks, the models and mimics evolve to higher values, moving away from the predators again. This repeats again at the end, although sooner. This is because predators are not able to store as much excess energy when attacking the mimics a second time.

3.2 Circular colour system

The three graphs in Figure 3.5 show the evolution of all three species in a run with the circular colour system from Section 2.2, while all other parts of the model remain the same. A summarized version of the three can be seen in Figure 3.6. The visibility values now range from -100 to 100, meaning the middle of the graphs represent camouflage, and the top and bottom represent essentially the same point. The run shown in this graph was conducted for 200,000 ticks instead of 50,000 like for the previous colour system, as some interesting patterns are visible only later in the simulation.

The models start at a visibility value of $-100/100$, and the mimics start at 0. In a typical run with these settings, the mimics quickly evolve through both negative and positive values, reaching the same colour as the models around 15,000 ticks. The two prey species follow nearly identical paths from 30,000 ticks onwards, in which the models and mimics cycle around the colour wheel. Some mimics benefit from the camouflage enough to stay alive for a while at the start, resulting in a lingering population at visibility 0. In this run, the predators are approaching from lower values, causing the prey agents to cycle around the colour wheel anti-clockwise (i.e. upwards in the graphs). In half of the runs, they will cycle clockwise instead.

Once the prey agents reach a visibility level close to 0, seen in figures 3.5 and 3.6 after about 120,000 ticks, they are protected by both mimicry and camouflage, and they linger here before continuing the cycle. This does not happen every time, but always around camouflaged values. While the models and mimics seem to follow a path from quite early on in the simulation, the predators have a much more erratic evolution pattern. While their mean from Figure 3.6 is not as clear, the three graphs from Figure 3.5 clearly show the predators and prey agents avoiding each other. The predators who eat models do not survive. When predators get close to the mean visibility of the prey agents, they might get lucky and only catch mimics, allowing them to survive longer. However, many predators either catch a model or have a visibility level too far away to restore their energy. This means that death and reproduction happen very frequently, creating the streaks seen in Figure 3.5 and the chaotic mean in Figure 3.6.
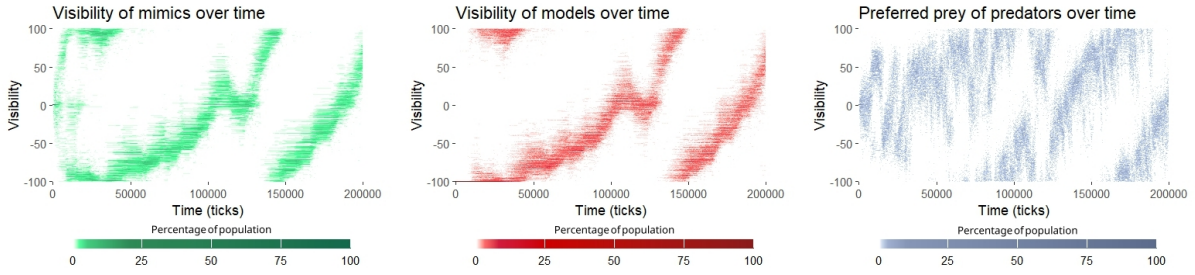
Figure 3.5: Heat maps for the values of the inheritable traits of each of the three species. Data from a run of 200,000 ticks, using the colour wheel system. Other settings are same as described in Section 2.4. Darker colours represent more agents having that visibility level during that tick.
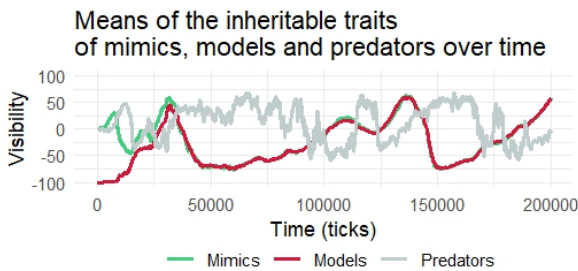

Figure 3.6: Combinations of the graphs in Figure 3.5, showing the means of the inheritable traits of the agents.
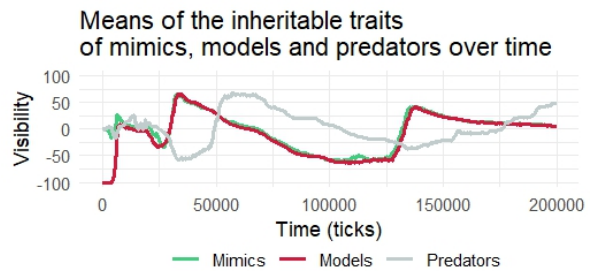

Figure 3.7: The means of the species in a run where neither the models nor mimics are dangerous to the predators, with the circular colour system.

3.2.1 Random starting values

Nearly identical patterns occur when the starting values of any combination of the species is set to random. Although the start of the graphs will look different and the point of convergence might be somewhat lower when the models start with random values, the cycling patterns eventually emerge nonetheless. Other ratios of model to mimic carrying capacities also show similar results. Only when there are not enough mimics to satiate the predators, or a species goes extinct for another reason, does the pattern not occur.

3.2.2 Non-lethal models

When the models are harmless, mimicry does not occur at high visibility. This is shown in Figure 3.7. Initially, mimics evolve away from their exact start at 0, as the predators also start at this value. The mimics do not move as extremely as in the lethal-model simulation however, and stay around

values close to 0 as much as possible. The models are safe with a visibility of 100 at first, but are attacked as well once the predators spread out. When this happens, the models quickly evolve towards camouflage, as these are the most advantageous in this system, joining the mimics. Once the mimics and models have the same colour, they start evolving in a cyclical way similar to the lethal-model simulation. This run shows a clockwise movement through the colour wheel (or downwards in the graph), but this does not happen every time, and is completely random depending on which way the predators have happened to evolve.

4 Discussion

4.1 Linear colour system

Experiments with harmless (i.e. non-lethal) models show that camouflage conveys clear evolutionary

advantages (Figure 3.4), as both prey agents evolve towards low visibility levels. When the models are lethal, the prey agents evolved towards higher visibility values instead, the advantage of mimicry outweighing that of camouflage.

The models and mimics both evolve aposematic colouration (high visibility values), even when all starting values were set to random. Predators learn to avoid aposematic models before camouflaged ones, as they have a higher chance of eating prey agents not protected by camouflage. This shows that the colour system allowed warning colourations to work within the ABM and that aposematic mimicry is more advantageous to mimics than camouflage within this simulation. Aposematic mimicry even occurred when there were only a very small number of models. Although this could be somewhat unrealistic due to the high reproduction rate, it shows evolutionary learning is very strong. When tested with the butterfly model from Wilensky, such low values for the number of models did not result in mimicry. Models would reproduce at a similar rate and stay alive, but predators would not learn to avoid a certain colour.

It could be that the stable mimicry-like situation of Figure 3.1 only emerged because of edge effects, as Franks predicted (2005). However, it might be argued that this effect is realistic, as snakes would not be able to evolve an even brighter red colour. Other colours would be possible, but many of the predators preying on coral snakes are colourblind (Brattstrom, 1955), which might limit the possibilities. Alternatively, the patterns could be changed, but as the plastic replica field studies showed (Brodie, 1993; Buasso et al., 2006; S. M. Smith, 1975, 1977), predators showed aversion to a wide range of ringed patterns. Perhaps the coral snake pattern really is an edge (or instead a corner) case in the evolution of snake patterns.

4.2   Circular colour system

The circular system showed mimicry-like results as well, since there was a clear difference between the start of the simulation with harmless models and the start of the one with dangerous models. When the models are dangerous, the mimics evolve towards the models, otherwise the mimics prefer to stay camouflaged and the models evolve towards the mimics instead. Predators in this ABM have

no way of evolving a resistance or defence to the dangers of the models, so the only way for them to survive and reproduce is to get lucky and eat mimics, requiring their species to 'chase'. Once the models and mimics share a colour, no matter whether the models are dangerous, they start circling the colour wheel due to the chasing predators. This circling is most likely not realistic, as coral snakes have had their brilliant red-black banding for millions of years (Rabosky et al., 2016).

The mean of the predators in the non-lethal-model simulation moves a lot more smoothly than in the lethal-model version, which is very chaotic. In the former simulation, predators can only die due to starvation. Since predators are all born with energy, they live for at least 200 ticks, causing evolution to happen quite slowly. In the other simulation, models can kill the predators at any time. The fast deaths and reproductions cause the mean preying colour of the predators to change quickly. For a similar reason, the relationship between the predator and prey agents changes. The predators are forced to stay behind the prey agents in the non-lethal-model simulation because they cannot evolve any faster. In the lethal-model simulation, they remain behind the prey agents because the chance of dying to a model is much higher when their preying mean is very close to the mean visibility of the models.

These two main differences show ways lethal agents can affect the predator evolution. While the colour wheel might not have been the right choice for this simulation, it still shows lethal agents can act as models for a mimicry system similar to Batesian mimicry.

4.3   Future extensions

ABMs are meant to be kept as simple as possible in order for it to be as general as possible. Some of these simplifications have caused interesting behaviours to emerge from this ABM, but more research is necessary to properly assess whether any conclusions can be drawn from those or whether other implementations would be more appropriate. The following is a list of changes or extensions that could be interesting to implement in the model as future research.

- While this thesis is in favour of Batesian

mimicry in coral snakes, it does not disprove Emsleyan/Müllerian mimicry. The harmless snake could be replaced by unpalatable but not lethal snakes, or these could be added as a third species. This combination could compare deception detection through evolutionary biases and learning from experience. It would be interesting to see which species would act as the model between these.

- While the linear colour system showed interesting results, this could be due to the prey agents being driven into a corner. The colour wheel system also has its issues, where instead of a corner, the agents are continually driven to a new colour. The way the colour system is defined determines the way the agents will evolve. A third colour system, or a combination of colour and pattern could be used to further investigate the implications of this.

- It has been assumed that predators have a certain range within which they can recognise agents as edible prey. Other options could be explored, such as a system where a predator recognises certain colours as inedible instead. This was briefly explored in the development of this model, in which it seemed to behave quite similarly to the preference system, especially with the circular colour system. This change would be especially interesting when paired with a change in colour system.

- Predator agents are currently capable of storing unlimited energy, which leads to a lot of predators gaining high energy levels and producing offspring for a long time. Increasing the amount of energy lost per tick or decreasing the amount of energy gained by eating a prey agent would cause the predators to quickly go extinct. Limiting the amount of energy they can store would be a viable alternative to this.

- The models were able to create a safe space even when there were very few of them due to their high reproductive chance. There would nearly always be the maximum number of agents for any given species. This might suggest the carrying capacity to be too abstract for this ABM. A common way agents reproduce in ABMs is to do so based on their energy level. They need to have been alive for a while and successful enough before they are able to create offspring. This was not used in this model to keep it as simple as possible, but could be added to avoid situations in which a single surviving agent can repopulate the species within just a few ticks.

5 Conclusion

In all results where the model was lethal, the mimics evolved towards the models and eventually reached the same colour, becoming indistinguishable to potential predators, benefitting from this situation. Especially the simulation with the linear colour system (Figure 3.1) shows a situation very similar to real life mimicry, suggesting that lethally defended species are indeed able to benefit from being aposematic and additionally can serve as models for a harmless mimic like in Batesian mimicry.

References

Arnold, E. (1984). Evolutionary aspects of tail shedding in lizards and their relatives. *Journal of Natural History*, *18*(1), 127–169. https : / / doi . org / 10 . 1080 / 00222938400770131

Bates, H. W. (1861). *Contributions to an insect fauna of the amazon valley. Lepidoptera : Heliconidae.* https://doi.org/10.5962/bhl.title.9486

Bradley, S., & Deavers, D. R. (1980). A re-examination of the relationship between thermal conductance and body weight in mammals. *Comparative Biochemistry and Physiology Part A Physiology*, *65*(4), 465–476. https : / / doi . org / 10 . 1016 / 0300 - 9629(80)90060-2

Brattstrom, B. H. (1955). The coral snake 'mimic' problem and protective coloration. *Evolution*, *9*(2), 217. https://doi.org/10.2307/2405591

Brodie, E. D., III. (1993). Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. *Evolution*, *47*(1), 227. https : / / doi . org / 10.2307/2410131

Buasso, C. M., Leynaud, G. C., & Cruz, F. B. (2006). Predation on snakes of Argentina: Effects of coloration and ring pattern on coral and false coral snakes. *Studies on Neotropical Fauna and Environment*, *41*(3), 183–188. https://doi.org/10.1080/01650520600630725

Bucaretchi, F., De Capitani, E. M., Vieira, R. J., Rodrigues, C. K., Zannin, M., Da Silva, N. J., Casais-E-Silva, L. L., & Hyslop, S. (2016). Coral snake bites (Micrurus spp.) in Brazil: A review of literature reports. *Clinical Toxicology*, *54*(3), 222–234. https://doi.org/10.3109/15563650.2015.1135337

Da Silva, N. J., & Aird, S. D. (2001). Prey specificity, comparative lethality and compositional differences of coral snake venoms. *Comparative Biochemistry and Physiology Part C Toxicology Pharmacology*, *128*(3), 425–456. https://doi.org/10.1016/s1532-0456(00)00215-5

Dunn, E. R. (1954). The coral snake "mimic" problem in Panamá. *Evolution*, *8*(2), 97–102. https://doi.org/10.2307/2405635

DuVal, E. H., Greene, H. W., & Manno, K. L. (2006). Laughing falcon (Herpetotheres cachinnans) predation on coral snakes (Micrurus nigrocinctus). *Biotropica*, *38*(4), 566–568. https://doi.org/10.1111/j.1744-7429.2006.00162.x

Emsley, M. G. (1966). The mimetic significance of Erythrolamprus aesculapii ocellatus Peters from Tobago. *Evolution*, *20*(4), 663–664. https://doi.org/10.2307/2406599

Franks, D. W. (2005). *Modelling the evolution of warning signals and mimicry with individual-based simulations.* University of Leeds. https://etheses.whiterose.ac.uk/1324/

Greene, H. W., & McDiarmid, R. W. (1981). Coral snake mimicry: Does it occur? *Science*, *213*(4513), 1207–1212. https://doi.org/10.1126/science.213.4513.1207

Hecht, M. K., & Marien, D. (1956). The coral snake mimic problem: A reinterpretation. *Journal of Morphology*, *98*, 335–365. https://doi.org/10.1002/jmor.1050980207

Loeffler-Henry, K., & Sherratt, T. N. (2021). A case for mutualistic deceptive mimicry. *Biological Journal of the Linnean Society*, *133*(3), 853–862. https://doi.org/10.1093/biolinnean/blaa219

Mertens. (1956). Das Problem der Mimikry bei Korallenschlangen. *Zoologische Jahrbucher, Abteilung für Systematik, Ökologie und Geographie der Tiere*, *82*, 541–576.

Moore, T. Y., Danforth, S. M., Larson, J. G., & Rabosky, A. R. D. (2020). A quantitative analysis of Micrurus coral snakes reveals unexpected variation in stereotyped anti-predator displays within a mimicry system. *Integrative Organismal Biology*, *2*(1). https://doi.org/10.1093/iob/obaa006

Müller, F. (1878). Ueber die Vortheile der Mimicry bei Schmetterlingen. *Zoologischer Anzeiger*, *1*, 54–55.

Pasteur, G. (1982). A classification review of mimicry systems. *Annual Review of Ecology and Systematics*, *13*, 169–199. https://doi.org/10.1146/annurev.es.13.110182.001125

Pough, F. H. (1988). Mimicry of vertebrates: Are the rules different? *The American Naturalist*, *131*, S67–S102. https://doi.org/10.1086/284767

Rabosky, A. R. D., Cox, C. L., Rabosky, D. L., Title, P. O., Holmes, I. A., Feldman, A., & McGuire, J. A. (2016). Coral snakes predict the evolution of mimicry across new world snakes. *Nature Communications*, *7*(1). https://doi.org/10.1038/ncomms11484

Reddingius, J. (1970). Models as research tools. *Dynamics of populations. Proceedings of the Advanced Study Institute for Dynamics of Numbers in Populations, Oosterbeek*, 64–74.

Ritland, D. B., & Brower, L. P. (1991). The viceroy butterfly is not a Batesian mimic. *Nature*, *350*(6318), 497–498. https://doi.org/10.1038/350497a0

Savage, J. M., & Slowinski, J. B. (1992). The colouration of the venomous coral snakes (family Elapidae) and their mimics (families Aniliidae and Colubridae). *Biological Journal of the Linnean Society*, *45*(3), 235–254. https://doi.org/10.1111/j.1095-8312.1992.tb00642.x

Sawaya, R., Marques, O., & Martins, M. (2008). Composition and natural history of a cerrado snake assemblage at Itirapina, Sao Paulo State, southeastern Brazil. *Biota Neotropica*, *8*, 127–149. https://doi.org/10.1590/S1676-06032008000200015

Smith, N. G. (1969). Avian predation of coral snakes. *Copeia*, *1969*(2), 402. https://doi.org/10.2307/1442098

Smith, S. M. (1975). Innate recognition of coral snake pattern by a possible avian predator. *Science*, *187*(4178), 759–760. https://doi.org/10.1126/science.187.4178.759

Smith, S. M. (1977). Coral-snake pattern recognition and stimulus generalisation by naive great kiskadees (Aves: Tyrannidae). *Nature*, *265*(5594), 535–536. https://doi.org/10.1038/265535a0

Thomas, A., Ii, S., & Ruane, S. (2022). *Concepts and contentions of coral snake resemblance: Batesian mimicry and its alternatives* (tech. rep.). https://academic.oup.com/biolinnean/article/135/4/631/6513742

Van Zandt Brower, J. (1958). Experimental studies of mimicry in some North American butterflies: Part i. the monarch, Danaus plexippus, and viceroy, Limenitis archippus archippus. *Evolution*, *12*(1), 32. https://doi.org/10.2307/2405902

Wickler, W. (1968). *Mimicry in plants and animals.* McGraw-Hill. https://archive.org/details/mimicryinplantsa00wick/page/110

Wilensky, U. (1997). *NetLogo Mimicry model.* Center for Connected Learning; Computer-Based Modeling, Northwestern University, Evanston, IL. https://ccl.northwestern.edu/netlogo/models/Mimicry

Wilensky, U. (1999). *NetLogo* (Version 6.4.0.). Center for Connected Learning; Computer-Based Modeling, Northwestern University, Evanston, IL. https://ccl.northwestern.edu/netlogo/

Wilensky, U., & Rand, W. (2015, April 3). *An introduction to agent-based modeling: Modeling natural, social, and engineered complex systems with NetLogo.* MIT Press.