How to Design Experiments in Animal Behaviour*

13. Harmless Snakes Mimic Venomous Snakes to Avoid Predation, But Why Don't They Do Their Best?

Raghavendra Gadagkar

There are many examples of perfectly palatable animals resembling related unpalatable species and, thereby, avoiding attack by predators who have learnt or evolved to avoid the unpalatable species. To facilitate recognition by predators, unpalatable species often have warning colourations, which is what is mimicked by the palatable species. This form of mimicry is known as Batesian mimicry. While there are many well-documented examples of Batesian mimicry among butterflies and other arthropods, there are somewhat fewer examples amongst vertebrates, and even these examples are often debated. The coral snake mimicry system in North America, where non-venomous kingsnakes and milksnakes mimic venomous coral snakes, is one of the best-studied vertebrate examples of Batesian mimicry. However, it has also been debated for over a century. In this article, I will describe three experiments using plasticine replicas of the mimics designed to understand the effectiveness of their mimicry. These field experiments were performed in the natural habitats of the mimics, the models and their predators, by David W. Pfennig and his students and collaborators, in the states of Florida, North Carolina, South Carolina, and Arizona in the USA. The simple, clever, and low-cost experiments have significantly strengthened the hypothesis of Batesian mimicry in this system. They have also provided an unexpected new understanding of how mimics might evolve from cryptic ancestors through a process of gradual natural selection.

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Mimicry

Prey species have two diametrically opposite strategies to defeat their predators. They can be cryptic and avoid detection or recognition. A variety of fascinating mechanisms including background matching, disruptive camouflage, and countershading, have evolved in prey species to remain hidden from their predators.

Plants use solar energy to make biomolecules such as proteins, carbohydrates, and lipids. Plants, therefore, provide an attractive option for herbivores to derive all their nutrition by eating the plants and not bother with photosynthesis. Not surprisingly, plants have evolved adaptations to prevent, or make it difficult, for herbivores to consume them, and herbivores have evolved adaptations to improve their chances of finding, eating, and digesting the plants. In this evolutionary arms-race, plants and herbivores are continuously chasing each other to win the battle for survival. But the herbivores (prey) themselves are an attractive option for carnivores (predators) to derive their nutrition by eating them. And of course, prey and predators have also evolved adaptations and counter-adaptations in their mutual battle for survival. The evolutionary arms race between prey and predators becomes more exciting because the predators can literally chase their prey and catch them. Prey species have two diametrically opposite strategies to defeat their predators. They can be cryptic and avoid detection or recognition. A variety of fascinating mechanisms including background matching, disruptive camouflage, and countershading, have evolved in prey species to remain hidden from their predators [1].

A diametrically opposite strategy is for the prey to become super-conspicuous. But how can this help? The secret is that this is only the second part of a dual strategy. The first part is to become unpalatable, toxic, or develop ways of biting or stinging, to injure or inject venom. Being unpalatable alone is insufficient because it usually comes too late in the sequence of events—the prey has already been captured, injured, or eaten. To make unpalatability profitable, predators have to be given an opportunity to recognize dangerous prey and avoid messing with them. This can be accomplished by being super-conspicuous. The super-conspicuousness is most often achieved through the evolution of aposematic (warning) colouration. Aposematic colouration is well known in many prey species. There is plenty of evidence that predators come to avoid aposematic prey either by a process of learning in their

lifetimes or by the evolution of an instinct to avoid them.

My alert readers would have already recognised that there is a potential problem in explaining the initial evolution of aposematism. The first individuals to develop warning colouration must have had to face a double whammy. They would have been more conspicuous than their wild-type, cryptic, counterparts, and their predators would not yet have acquired the necessary behavioural or innate adaptations to avoid eating them. It is of great historical interest that as early as 1958, Ronald A. Fisher suggested a solution to this problem which, we see in retrospect, is the forerunner of the modern theory of kin selection [2]. Fisher argued that if distasteful prey are gregarious larvae, for example, one may be eaten but the rest will be spared. And if the distasteful larvae are a large group of siblings, as it is not unlikely, then they all stand to benefit from the sacrifice of the one eaten. There is evidence for Fisher's idea, especially in the form of correlations between the evolution of chemical defences and the evolution of gregariousness.

Such co-evolution of chemical defences and warning colouration in some species opens up an evolutionary opportunity for other species to cheat—to evolve the relatively inexpensive warning colouration without backing it up with the more expensive chemical defences. Thus, palatable species come to superficially resemble unpalatable species, a phenomenon that is known as Batesian mimicry, named after the English naturalist Henry Walter Bates (1825–1892). Bates discovered many examples of mimicry and proposed the hypothesis mentioned above for their evolution. There is also the related phenomenon of Müllerian mimicry, named after the German zoologist and naturalist Johann Friedrich Müller (1821–1897). Müller proposed the idea that multiple unpalatable species may evolve similar warning colouration (mimic each other) and thus reinforce the benefits of being avoided by their predators. It is noteworthy that Müller provided a mathematical model, one of the first mathematical models in biology, to show how Müllerian mimicry might work. There are many examples of both Batesian and Müllerian mimicry, especially among

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insects, and some model species may have both Batesian and Müllerian mimics resembling them. Indeed, butterflies provide a Klondike of examples for both Batesian and Müllerian mimicry [3]. In addition to butterflies, examples of mimicry, either as models or as mimics have been found, perhaps we should say hypothesised, in a large number of animal and even plant taxa. These include millipedes, moths, beetles, ants, bees, wasps, mantids, hoverflies, crabs, cuttlefish, octopuses, spiders, fish, toads, lizards, snakes, birds and mammals, and also orchids and some other angiosperm families [4, 5].

Coral Snakes

Compared to the arthropods, mimicry has been less well studied and is considerably more controversial, among the vertebrates. Here, we will focus on coral snakes, a group in which mimicry has been extensively studied and hotly debated for over a century. Coral snakes belong to the family Elapidae (the same family as such deadly species as cobras, kraits, and sea snakes). Coral snakes are believed to have originated in the Old World, with about 16 extant species present today, and diversified in the New World with about 65 extant species today. In North America, coral snakes belonging to the genera *Micrurus* and *Micruroides* are strikingly conspicuous with their bright, red, yellow/white and black bands and are also highly venomous. Their venom contains powerful neurotoxins. These snakes are hypothesised to serve as models for several co-occurring non-venomous snakes such as kingsnakes and milksnakes (genus *Lampropeltis*), which resemble the venomous coral snakes to varying degrees (*Figure* 1). The resemblance is not always perfect, and one can tell them apart with some effort, at least when not confronted by a live specimen in the wild! People in the USA, where the native coral snakes have red and yellow/white bands that touch, but where the native kingsnakes and milksnakes have red and yellow/white bands that are separated by black bands, have invented mnemonics to aid in their distinction such as, "Red touches yellow, you're a dead fellow; Red touches black, you're okay Jack". However, these

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The Models	The Mimics
Micrurus fulvius (Eastern coral snake, photo: Wayne Van Devender)	*Lampropeltis elapsoides* (Scarlet kingsnake, photo: David W. Pfennig)
Micruroides euryxanthus (Sonoran coral snake, photo: David W. Pfennig)	*Lampropeltis pyromelana* (Sonoran mountain kingsnake, photo: David W. Pfennig)

mnemonics do not work in Central and South America, where coral snakes (and their mimics) can exhibit either pattern, so it is best to avoid both. Avoiding both is exactly what their predators also seem to do. Therein lies the advantage for the harmless mimics, who gain the benefit of being avoided by predators, without paying the cost of producing venom or developing the fangs and other paraphernalia needed to inject venom. Kingsnakes and coral snakes are, therefore, a textbook example of Batesian mimicry [6].

Figure 1. Photos of two venomous coral snakes that serve as models (left) and their two corresponding non-venomous mimics (right).

Is Coral Snake Mimicry a Just-So-Story?

It has sometimes been suggested that the non-venomous, brightly coloured shieldtail snakes (family: Uropeltidae) in India are Bate-

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sian mimics of the local coral snakes. On closer examination, it appears very unlikely that uropeltid snakes in India are mimics of our coral snakes. Their resemblance is very poor, their range overlap is not extensive, and where they overlap, the coral snakes are very rare. Moreover, recent fascinating work by Ullasa Kodandaramaiah and his student, at the Indian Institute of Science Education and Research, Thiruvananthapuram has shown instead that the bright colours of shieldtail snakes are their own warning signals to predators not to mess with them—even though they are not venomous, they are very difficult to capture and require long handling times to process and eat them. Thus, unprofitability due to other causes, such as the need for long handling times, can also be signalled by the conspicuous colouration of prey which the predators learn to avoid [7, 8].

It is, therefore, essential to treat every example of mimicry as a hypothesis waiting to be tested. To claim Batesian mimicry involving specific model and mimic species is not easy. In most cases, the resemblance between the mimic and the model is based on human perception and not that of the relevant predators. We seldom know the evolutionary history of the model and mimic species and for how long they have overlapped in their distribution. We do not usually know the strength of the selective pressure exerted by the predators in the absence of the mimicry and the extent to which it is relieved by the adaptation of mimicry. We rarely know the relative frequencies with which the models and mimics should co-exist for there to be a significant advantage to the mimic without the predators learning (or evolving to "know") that they are being cheated. An even more complicated problem is whether there would be selective pressure on the model to subsequently evolve to become different from the mimic so that its defence against predation is not diluted. This plethora of unknowns makes testing the hypothesis of mimicry, especially Batesian mimicry, a challenge worthy of the most creative and skilled researchers.

The hypothesis that kingsnakes and milksnakes are Batesian mimics of coral snakes, in North America, has been held up to rigor-

ous scrutiny by both its proponents and its opponents for well over a century. The main contention of the critics has been that the proposed hypothesis of coral snake mimicry violates two theoretical predictions; predictions derived mainly from the study of mimicry in butterflies. These predictions are that mimics should not be found outside the geographical range of the models and that the models should be much more common than the mimics. On the face of it, these theoretical predictions sound entirely reasonable and are largely supported by the data on mimicry in butterflies. So, the question arises if the coral snake mimicry story is a just-so-story. Proponents of the coral snake mimicry hypothesis have taken up these challenges in good spirit and have now studied coral snake mimicry in North America extensively over many decades [9]. And that is what makes the story of coral snake mimicry so rich and interesting to survey in retrospect.

Here, I will describe three experiments that have played a significant role in generating confidence in the validity of the coral snake mimicry hypothesis in North America. As the readers of this series will understand, I have chosen these experiments primarily because of their simplicity, cleverness and low-cost. David Pfennig performed these experiments along with his students and collaborators. David Pfennig is now Professor of Biology at the University of North Carolina, Chapel Hill in the USA. He began his research career investigating nestmate discrimination in paper wasps, and now he mainly focusses his research on the role of developmental plasticity in evolution, the role of competition in generating and maintaining biodiversity, and Batesian mimicry in snakes. He recently told me that "The mimicry stuff was one of my 'side projects' that I just did with some undergrads and former grad students for the fun of it, so I'm always happy to talk about these studies. These were indeed simple and inexpensive experiments that anyone can perform."

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Figure 2. David W. Pfennig (left) holding a scarlet kingsnake, William Harcombe (middle) and Karin S. Pfennig (right) holding a Texas horned lizard (*Phrynosoma corunutum*) near Portal, Arizona, where they all conducted some of their field experiments.

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Does Protection for the Mimics Depend on the Presence of the Models in the Vicinity?

If the hypothesis that the non-venomous kingsnakes are Batesian mimics of the venomous coral snakes is valid, then the extent of protection that the mimics get from predator attacks must depend, at least to some extent, on the presence of the model species in their vicinity. David Pfennig (*Figure* 2, left), his student William Harcombe (*Figure* 2, middle), and his wife and collaborator Karin Pfennig (*Figure* 2, right) have put this prediction to the test using simple and inexpensive field experiments. At the time of the study, William Harcombe was an undergraduate doing his honours thesis (he is now Associate Professor in the College of Biological Sciences, the University of Minnesota in midwestern United States, currently studying the evolutionary ecology of microbial communities). Karin Pfennig is also a Professor of Biology at the University of North Carolina, Chapel Hill, and she studies the role of behaviour in the origin, maintenance and distribution of biodiversity, including the role of mate choice in the formation and maintenance of species boundaries.

In North and South Carolina, the trio studied the mimicry system of the scarlet kingsnake *Lampropeltis elapsoides* (*Figure* 1, top right), which resembles the eastern coral snake *Micrurus fulvius* (*Figure* 1, top left). In Arizona, they studied the mimicry system of the Sonoran mountain kingsnake *Lampropeltis pyrome-*

Figure 3. A plasticine replica, *in situ* in North Carolina, of a scarlet kingsnake, a Batesian mimic of the eastern coral snake.
(Photo: David W. Pfennig)

lana (*Figure* 1, bottom right), which resembles the Sonoran coral snake *Micruroides euryxanthus* (*Figure* 1, bottom left). Their experimental strategy was to present naturally occurring, free-ranging predators (mostly carnivore mammals, such as grey foxes, racoons, coyotes, and black bears) with artificial replicas of snakes that either did or did not resemble the relevant mimic, and see whether the predators preferentially avoided those replicas that resembled the mimics. They did so by constructing thousands of these replicas and placing them in natural areas. These snake replicas were in the form of 1.5 cm × 18 cm cylinders made of pre-coloured, non-toxic plasticine, which was threaded onto S-shaped wires (*Figure* 3). The replicas were either made to resemble the mimic species (referred to as ringed replicas) in the locality of study (scarlet kingsnake or Sonoran kingsnake, as the case may be) or not to resemble the mimics. The latter, which served as controls, were of two kinds; one had stripes with identical colours and proportions as the mimics (but not the same patterns), and the other was plain brown. The former control served to test whether predators avoided any brightly coloured snake, whereas the latter control served to test whether predators avoided any snake (regardless of the colour pattern).

A triplet of three replicas, one resembling the mimic and one of each of the two control types, were placed 2 m apart from each other in the natural habitat of the predators. At each study site, they placed 10 triplets, 75 m apart, along a transect. We must realise that the predators may or may not consider it worthwhile to attack plasticine replicas; they may realise that it is not a snake at all. The absolute number of attacks on the plasticine replicas is, therefore, not very informative. However, the proportion of attacks on the replicas resembling the mimics (out of the total number of attacks on all the replicas, including the controls) would be informative. If this proportion is low, then it means that the predators are avoiding the replicas that resemble the non-venomous mimic species, which in turn resemble the venomous model species. At the end of the experiment, the replicas were collected, brought to the lab, and a person who was unaware of the location of the replicas checked them for signs of predation by noting impressions of teeth, claw, or beak marks on them.

In North/South Carolina, they conducted the experiment at eight sites in which the model species, namely the eastern coral snake *Micrurus fulvius* occurs (sympatric sites), and eight sites in which it does not occur (allopatric sites), using a total of 420 replicas. The study sites were 16–420 km apart, and the allopatric sites were all more than 80 km outside the range of the venomous model species. Here, sympatry and allopatry refer to whether or not the distribution of the mimic overlaps (sympatry) or does not overlap (allopatry) with the distribution of the model species. At the end of 4 weeks, 25 (6.0%) of the replicas had been attacked. Although this absolute number is very small, a significantly greater proportion of ringed replicas (those that resembled the mimics) were attacked in the allopatric sites (mean ± s.e.m. = 0.654 ± 0.107) compared to the corresponding proportion in the sympatric sites (mean ± s.e.m. = 0.083 ± 0.116) ($P < 0.009$, 2-tailed Wilcoxon two-group test).

In Arizona, they conducted the experiment at 24 sites along an elevational gradient (from 1,204 m to 2,866 m), 3–100 km apart from each other, using a total of 720 replicas. Since the distri-

bution of the venomous Sonoran coral snake *Micruroides euryx-anthus* is restricted to elevations below 1,770 m, they thus had 14 sympatric and 10 allopatric sites. At the end of two weeks, 49 (6.8%) of the replicas were attacked. Again, although the absolute numbers were small, a significantly greater proportion of ringed replicas were attacked in allopatric sites (0.496 ± 0.078) compared to the proportion in the sympatric sites (0.138 ± 0.060) ($P < 0.006$, 2-tailed Wilcoxon two-group test). With the Arizona data, they were also able to compare the rates of attacks on the ringed replicas with what is expected by chance. Their data showed that the proportion of ringed replicas attacked in the sympatric sites was significantly less than expected by chance ($P = 0.010$) whereas the proportion of ringed replicas attacked in the allopatric sites was not different from the chance expectation ($P = 0.188$) (2-tailed Wilcoxon signed-rank test). Notice that since there were two control replicas (striped and plain brown) for every ringed replica, the chance expectation for attacks on ringed replicas is 0.33. Looking at their data in another way they plotted the proportion of ringed replicas attacked as a function of the latitude of the study site in North/South Carolina and elevation of the study site in Florida and found a significantly positive slope in both cases. Coral snakes decrease in abundance with increasing latitude in the Carolinas and they decrease with increasing elevation in Florida (*Figure* 4).

Taken together, these results show that the ringed replicas were attacked less by predators in localities where the model snakes are present or abundant, and attacked more in localities where the model species are absent or rare. We can infer from this that non-venomous mimics are likely to get protection from predators due to their resemblance to the venomous model species. The results of this experiment take us a step further in validating the hypothesis that scarlet kingsnakes and Sonoran mountain kingsnakes are Batesian mimics of the Eastern and Sonoran coral snakes, respectively, and give us confidence that it is not a just-so-story [10].

But the question of why the mimics have not been completely eliminated in localities where their venomous models are absent

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Figure 4. Frequency-dependent mimicry. The proportion of carnivore attacks on ringed replicas of scarlet kingsnakes (top left; a mimic of eastern coral snakes) and Sonoran mountain kingsnakes (top right; a mimic of Sonoran coral snakes) increased with **(a)** latitude (y = -13.314 + 0.391x, P < 0.035, R^2 = 0.345) and **(b)** elevation (y = 0.329 + 0.00032x, P < 0.014, R^2 = 0.310). The horizontal dashed line indicates the proportion of attacks on ringed replicas expected under randomness. The vertical dashed line indicates the maximum latitude and elevation for coral snakes in North Carolina and Arizona, respectively.
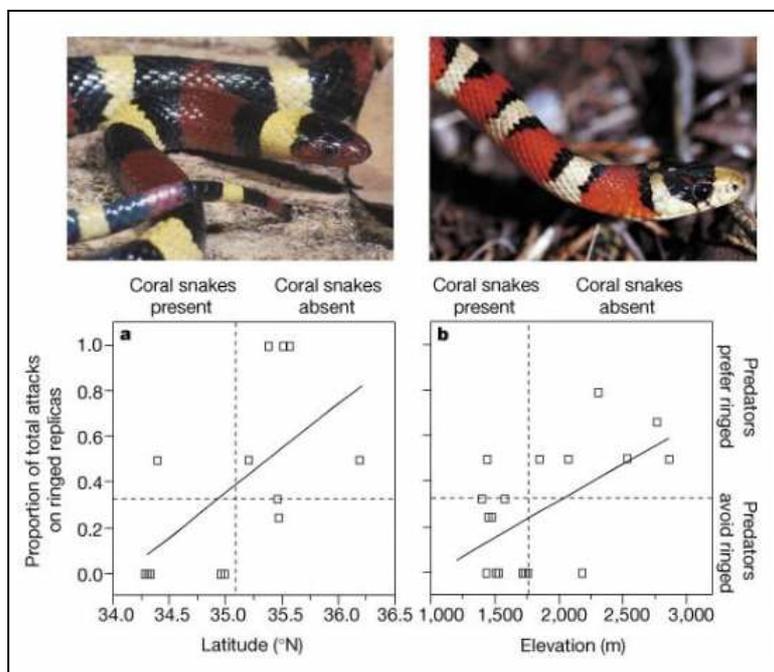
[Reprinted with permission from: D W Pfennig, W R Harcombe and K S Pfennig, Frequency-dependent Batesian mimicry: Predators avoid look-alikes of venomous snakes only when the real thing is around, *Nature*, 410, 323, 2001]

or rare remains unanswered. I encourage my readers to come up with plausible hypotheses to answer this question. If, after doing so, you read up the more recent research on coral snake mimicry, you will see that several of your hypotheses have been put to the test, and some have been vindicated [11, 12]. I assure you that it will be much more fun to read the literature after you have come up with your own hypotheses than do so without putting your own ideas at stake.

Why Aren't Mimics Perfect?

We might think that natural selection would act to make mimics resemble their models as closely as possible. Indeed, we might think that imperfect resemblance is evidence against the hypothesis that the mimic species we are studying is a Batesian mimic of the proposed model species. Such reasoning ignores other factors which may be more important for the survival of the mimic. Besides, why should we imagine that a perfect mimic always sur-

vives better than an imperfect mimic? If we think of mimicry as an evolutionary game between the mimic, the model and the predator, we might expect much more complicated dynamics and many final outcomes. Thus, imperfect mimicry may not always be maladaptive or evidence against the hypothesis of mimicry. In this way of thinking, we can begin to hypothesize potential selective reasons for imperfect mimicry.

Imperfect mimicry may not always be maladaptive or evidence against the hypothesis of mimicry.

For example, we may propose the hypothesis that in places where the venomous model is very common, the predators are selected to be extremely careful and hence avoid approaching even something that looks vaguely like the model. In other words, imperfect mimics may get protection from predators in spite of their imperfection. On the other hand, where the model is quite rare, predators may not be strongly selected to be very careful because the chances of encountering the venomous snake are quite small. In such a situation, we may expect that imperfect mimics may be eaten and only the perfect mimics avoided by the predators. This line of argument, if realistic, would suggest a very counter-intuitive outcome. Where the models are common, mimicry should be imperfect, and where the models are rare, mimicry should be perfect. This, of course, is just arm-chair theorizing. There is no guarantee that it is realistic. But the fact that this hypothesis makes a rather counter-intuitive prediction makes it a powerful hypothesis, meaning that it is really worth testing. If its counter-intuitive prediction is upheld, we may have somewhat greater confidence in our hypothesis because the prediction was borne out in spite of the fact that there are many reasons why it should not—that is why it was counter-intuitive in the first place.

David Pfennig, along with his graduate student George Harper (*Figure* 5) decided to test the counter-intuitive prediction of this interesting hypothesis. They used the venomous eastern coral snake *Micrurus fulvius* (*Figure* 1, top left) and its model, the scarlet kingsnake *Lampropeltis triangulum elapsoides* (*Figure* 1, top right) mimicry system in Eastern North America. The model species is distributed in Florida and southern parts of Mississippi, Alabama, Georgia, South Carolina and North Carolina. The

Figure 5. George Harper in the field in North Carolina while he was a graduate student with David Pfennig at the University of North Carolina, Chapel Hill. He is now an Associate Professor in Hendrix College, in Arkansas, USA.
(Photo: David Pfennig)

mimic species has a much wider distribution, including Florida, almost the entire region of all the other above-mentioned states as well as Tennessee and parts of Kentucky and Virginia (*Figure* 6). The experiments described in the previous section of this article have already shown that the mimics get little or no protection from predators when they are outside the range of the model (allopatric). And, it is expected that the model species would decrease in abundance at the edges of its distribution. Harper and Pfennig, therefore, decided to set up some of their study sites in Florida, which is deep inside the distributional range of the model, and other study site in North Carolina, which is at the very edge of its distribution. The mimic species occur throughout, and it may be said to show deep sympatry with the model in Florida and edge sympatry in North Carolina. Based on the counter-intuitive prediction of the hypothesis outlined in the previous paragraph, Harper and Pfennig had three questions to answer: (1) Is the mimic relatively imperfect or more variable in Florida compared to North Carolina? (2) Is the model indeed more abundant in Florida than in North Carolina? (3) Is the pre-
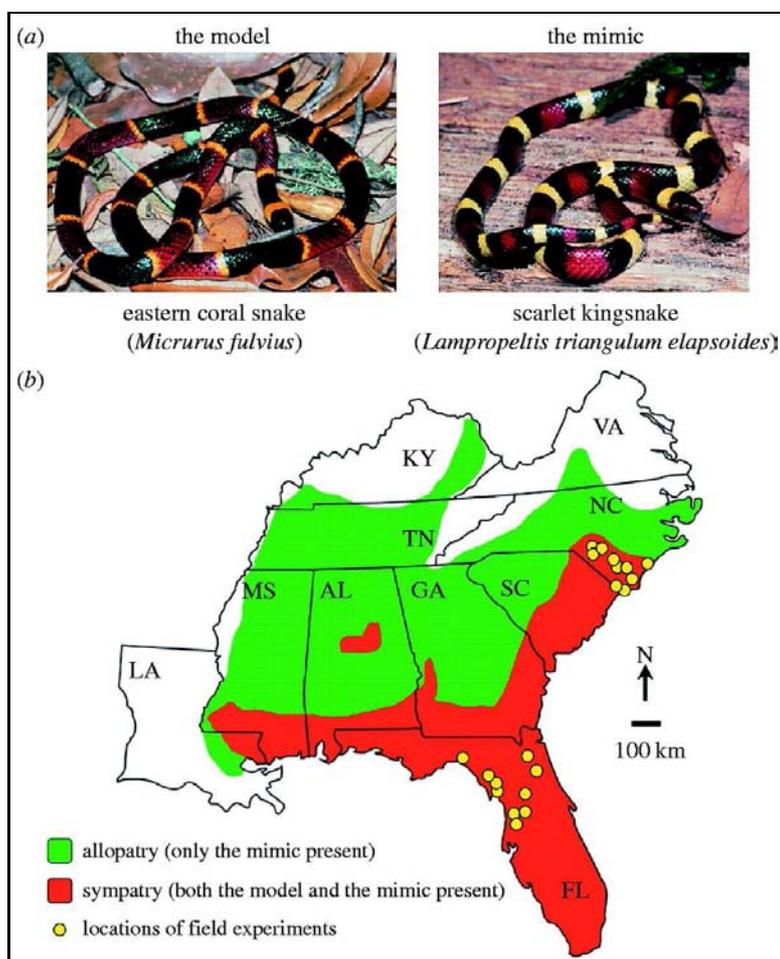
Figure 6. **(a)** The non-venomous scarlet kingsnake (*L. t. elapsoides*) mimics the highly venomous eastern coral snake (*M. fulvius*). **(b)** The geographical range of *L. t. elapsoides* (the mimic) greatly exceeds that of its model.
[Reprinted with permission from: G R Harper Jr. and D W Pfennig, Mimicry on the edge: why do mimics vary in resemblance to their model in different parts of their geographical range? *Proc. R. Soc. Lond. B*, Vol.274, pp.1955–1961, 2007.].

dation pressure on good and poor mimics different in Florida and North Carolina?

Is the mimic relatively imperfect or more variable in Florida compared to North Carolina?

As you can imagine, we cannot rely only on our perception of what is a good and what is a poor mimic. Moreover, the closeness in resemblance of the mimic should be in relation to the appearance of the model species in that particular area. Hence, Harper and Pfennig conducted a detailed morphometric analysis (a study
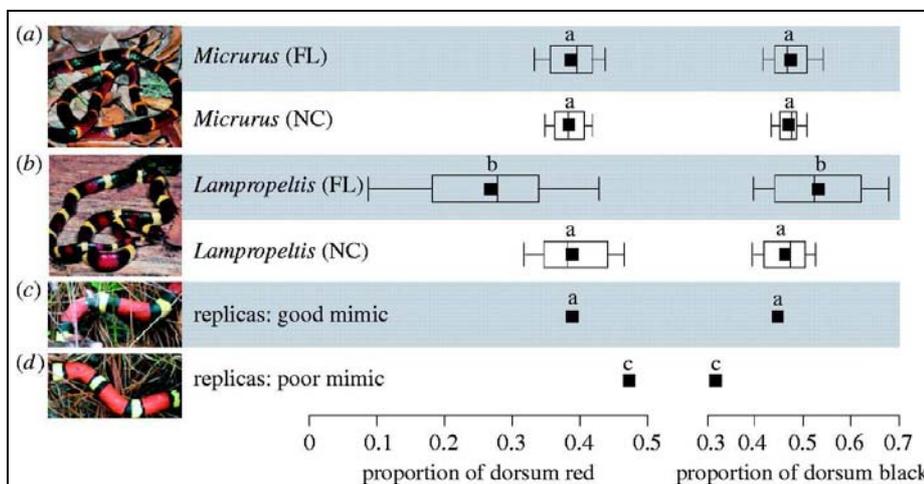
Figure 7. Comparison of two diagnostic traits for **(a)** the model (*Micrurus*) and **(b)** the mimic (*Lampropeltis*) from Florida (FL, deep sympatry) and North Carolina (NC, edge sympatry) and for **(c)** the good and **(d)** poor mimic replicas. Black squares show means. Box plots show 10th, 25th, 50th (median), 75th and 90th percentiles. Means with different superscripts are significantly different (P < 0.05; Tukey–Kramer HSD). [Reprinted with permission from: G R Harper Jr. and D W Pfennig, Mimicry on the edge: Why do mimics vary in resemblance to their model in different parts of their geographical range? *Proc. R. Soc. Lond. B*, Vol.274, pp.1955–1961, 2007.].

of the measures of external body parts) of both the model and the mimic. First, they photographed both species by placing them on a similar background. As part of his PhD thesis, George Harper had previously determined that two characteristics helped to differentiate between good and poor mimics. These were: (i) the proportion of the snake's mid-dorsum that is black, and (ii) the proportion of the snake's mid-dorsum that is red. Incidentally, he had come to this conclusion because these are the two patterns that break down in allopatry [11]; i.e., where the model is not present, and the predators attack the mimic. So, for each species, from each locality, they now calculated the proportions of red and black on the mid-dorsum. The results of their study can be seen in (*Figure* 7). For both traits, the model species did not differ between Florida and North Carolina. The mimics, however, differed between the two locations. In North Carolina (edge sympatry), the model and the mimic did not differ from each other, meaning that the mimicry was good. In Florida (deep sympatry), however, the mimic species was much more variable and significantly different from the model, meaning that the mimicry was not good. In other words, the answer to the first question is that mimicry is good in edge sympatry (where the model is rare) but poor in deep sympatry (where the model is common), just as predicted.

Is the model more abundant in Florida than in North Carolina?

To answer this rather difficult question, Harper and Pfennig counted the number of specimens of the model and mimic species in various museums. They also used some data which were available for North Carolina. Harper and Pfennig are conscious that this method of estimating abundance is not likely to be very precise in terms of absolute numbers of each species. Nevertheless, this method should give an unbiased estimate of the relative abundance of each species, which is what they were after. As it turns out, their numbers confirmed the common knowledge that the venomous coral snake is much more abundant in Florida than in North Carolina. They found that the ratios of the model to the mimic (more important than absolute numbers) differed significantly between Florida and North Carolina. Models outnumbered mimics in Florida (median of one model per mimic). By contrast, in North Carolina, mimics outnumbered the models (median of zero models per mimic). Thus, the second question was also answered in the affirmative.

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Is the predation pressure on good and poor mimics different in Florida and North Carolina?

To answer this question, Harper and Pfennig prepared plasticine replicas of the naturally occurring good and poor mimics. To construct their good mimics, they ensured that the proportions of black and red in the replica were not significantly different from the model and the mimic in North Carolina (where mimicry is more precise; see the first question above). Their replicas of the poor mimic were significantly different from (i) the models in both localities, (ii) their own plasticine replicas of the good mimics, (iii) the good mimics in North Carolina, but, as it happens, they were also different from the poor mimics in Florida. They nevertheless used their replicas of poor mimics for experimentation in both the localities because previous research had shown that the phenotype corresponding to these replicas could be regarded as a poor mimic.

Figure 8. Mean (s.d.) proportion of total attacks on each replica type in edge sympatry (North Carolina). The observed proportion of attacks only on replicas of good mimics was significantly (p < 0.05) less than 0.33 (dashed horizontal line), the value expected if predation attempts were random with respect to colour pattern.

[Reprinted with permission from: G R Harper Jr. and D W Pfennig, Mimicry on the edge: why do mimics vary in resemblance to their model in different parts of their geographical range? *Proc. R. Soc. Lond. B*, Vol.274, pp.1955–1961, 2007.]
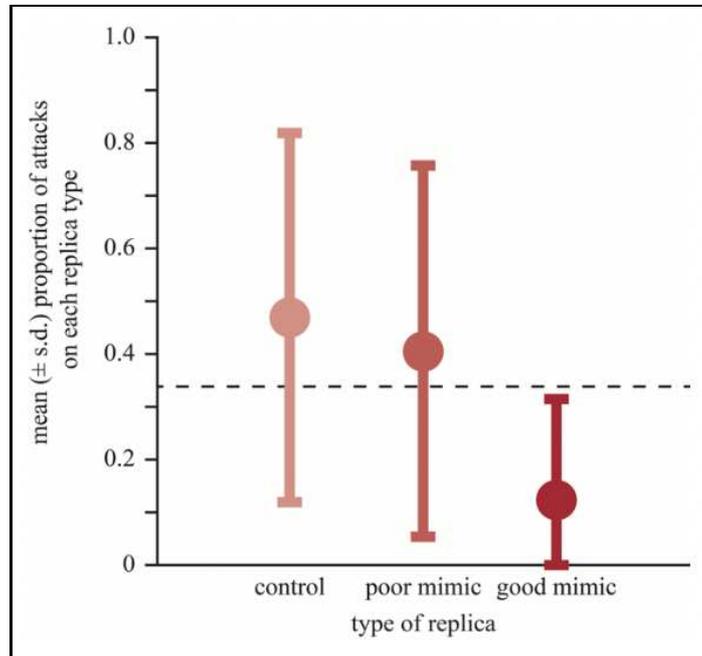
Choosing ten sites each in Florida (deep sympatry) and North Carolina (edge sympatry), they arranged triplets of replicas (with replicas of one good mimic, one poor mimic, and one control) at ten different points along the transect in each site. As before, a person without knowledge of the location of the replicas scored for predator attack marks (made by carnivores such as black bear, bobcat, coyote, fox or racoon) on all the replicas at the end of the experiment. They found that in North Carolina (edge sympatry), only the good mimics were attacked significantly less often than expected by chance (*Figure* 8). In Florida (deep sympatry), however, good and poor mimics were attacked equally frequently (data not shown). On the whole, it may be said that the predators distinguished between the good and poor mimics in North Carolina, but not in Florida.

Taken together, the three results show that the model is more abundant in Florida than in North Carolina, the mimics are more imperfect in Florida than in North Carolina, and that the predator did not discriminate between good and poor mimics in Florida but

did so in North Carolina. The counter-intuitive prediction is thus upheld. There indeed is a stronger selection to be a good mimic where the model is rare (North Carolina) than where the model is common (Florida). This counter-intuitive result should change how we imagine that the evolution of mimicry would work. As noted above, this result makes sense when we take into consideration all three actors: the model, the mimic, and the predator. Mimicry is a dynamic game played with three players over evolutionary time. Thus, mimics can be imperfect when selection for being perfect is relaxed in the presence of large numbers of the model species, which in turn makes predators very careful. And here, very careful means predators will avoid anything that even vaguely looks like the venomous model species. So, why don't mimics do their best? Because it is not really necessary for their survival when the models are common [13].

Taken together, the three results show that the model is more abundant in Florida than in North Carolina, the mimics are more imperfect in Florida than in North Carolina, and that the predator did not discriminate between good and poor mimics in Florida but did so in North Carolina.

How Do Mimics Evolve from Non-Mimics?

The counter-intuitive result obtained above that mimics tend to be much more precise when the model species are rare, but they tend to be imprecise when the model species is common, potentially solves another major evolutionary problem. This concerns how mimics can evolve from their cryptic ancestral species through natural selection. When any phenotype evolves by natural selection, this process is usually assumed to occur through a gradual step-by-step process involving many intermediate stages of the phenotype. The unsolved problem concerns how the intermediate phenotypes in such a gradual evolutionary process might survive in the context of mimicry. The intermediate stages in the evolution of mimicry are neither expected to have the benefit of crypsis (which they have given up) nor the benefit of perfect mimicry (which they have not yet attained). Therefore, predators should preferentially attack the intermediate forms so that evolution should not proceed any further. However, based on the result in the previous section, the hypothesis can now be proposed that intermediate forms survive and, therefore, can evolve further into better mimics in areas where their model species is abundant.

In technical language, the evolution of mimicry can be visualized on what is called 'the adaptive landscape', in which high points (or 'peaks') are phenotypes associated with high fitness and low points (or 'valleys') are phenotypes associated with low fitness.

In technical language, the evolution of mimicry can be visualized on what is called 'the adaptive landscape', in which high points (or 'peaks') are phenotypes associated with high fitness and low points (or 'valleys') are phenotypes associated with low fitness. These concepts of adaptive valleys and adaptive peaks were introduced by Sewall Wright, one of the three major architects of modern evolutionary theory, in his famous Shifting Balance Theory of Evolution [14]. If there is an adaptive valley between two adaptive peaks, then evolution by natural selection cannot easily cross the valley; to do so would require an individual to produce offspring with phenotypes that are associated with lower fitness than the parents, which is not favored by natural selection. Essentially, the problem with the evolution of mimicry is that crypsis on the one hand and mimicry on the other can each be thought of residing on different peaks on the adaptive landscape. How, then, can mimicry evolve from crypsis (which is generally assumed to be the ancestral condition) through the traditional process involving the accumulation of small genetic changes? After all, this process would require that a population must first cross a fitness valley associated with intermediate forms (for instance, an imprecise mimic). Such imprecise mimics should be poorly adapted and, therefore, not be able to cross the valley and reach the next adaptive peak (the one associated with more precise mimicry) where they would be well adapted to survive. Theoreticians generally overcome this problem by postulating so-called 'supergenes' which are supposed to bring about a major phenotypic change in one shot and allow their bearers to jump over the valley. This is exactly what theoretical models for the evolution of Batesian mimicry have proposed. While there is evidence for the role of such supergenes in the evolution of Batesian mimicry in butterflies [3], this need not be the case in all instances of mimicry. In the present context, the new hypothesis is that areas of high model abundance present a scenario where there is no adaptive valley between the adaptive peak of crypsis and the adaptive peak of perfect mimicry. If this hypothesis is correct, there is no need to postulate supergenes.

In the present context, the new hypothesis is that areas of high model abundance present a scenario where there is no adaptive valley between the adaptive peak of crypsis and the adaptive peak of perfect mimicry.

Figure 9. David Kikuchi on field work as Karin Pfennig (whom we met in the first experiment) and the Pfennig children, Katrina and Elsa, look on—what a great experience for the children and adults alike!

David Pfennig and another of his graduate students, David Kikuchi, set out to test this hypothesis using the coral snake mimicry system of the Eastern coral snake *Micrurus fulvius* and its mimic *Lampropeltis elapsoides*, both in Florida where the model species is abundant and in North Carolina where the model species is rare. The hypothesis predicted equal predation rates on cryptic species, poor mimics, and good mimics in Florida where the model is common. David Kikuchi (*Figure* 9) is now a Post-doctoral Research Fellow at the University of Bielefeld in Germany, and I had the pleasure of meeting him when he spent the academic year 2019–2020 at the Wissenschaftskolleg, Institute for Advanced Study in Berlin. First, they confirmed that the scarlet kingsnake is indeed likely to have evolved from cryptic ancestors. For this, they performed a test known as ancestral character-state reconstruction. This means they examined a recently published phylogeny of the scarlet kingsnake and its relatives, 31 species belonging to the tribe Lampropeltini. They determined the colour patterns of all the snakes represented in the phylogeny and found evidence that all species that had a strong mimetic resemblance to coral snakes were located in a single clade which in turn was derived from clades containing cryptic species [see *Figure* 2 in Suggested Reading 15]

Figure 10. Replicas of different snake phenotypes used to measure predation in the field, along with the species or subspecies of snake that each most closely resembled. **(a)** Cryptic phenotype, which resembled **(b)** the eastern milksnake, *L. t. triangulum* (photo by Roger W. Barbour); **(c)** intermediate phenotype, which resembled **(d)** the coastal plains milksnake, *L. t. temporalis* (photo by Richard D. Bartlett); **(e)** mimetic phenotype, which resembled **(f)** the scarlet kingsnake, *L. elapsoides* (inset: the eastern coral snake, *M. fulvius*, which *L. elapsoides* mimics; photos by Wayne van Devender).

[Reprinted with permission from: D W Kikuchi and D W Pfennig, High-model abundance may permit the gradual evolution of Batesian mimicry: An experimental test, *Proc. R. Soc. Lond. B*, Vol.277, pp.1041–1048, 2010.]

Next, the two Davids made plasticine replicas of three different phenotypes of the mimic, a cryptic phenotype which resembled the Eastern milksnake *Lampropeltis triangulum*, an intermediate phenotype which resembled the coastal plains milksnake *Lampropeltis temporalis*, and the mimetic phenotype which resembled the scarlet kingsnake *Lampropeltis elapsoides* (*Figure* 10). Perhaps I should mention a technical detail about the preparation of the replicas. As part of David Kikuchi's PhD thesis, he had previously gathered extensive morphometric data on the Eastern milksnake, *L. triangulum*. George Harper and David Pfennig (whose experiments we saw in the previous section) had obtained similar morphometric data on the mimetic kingsnake *L. elapsoides*. There is good reason to believe that the Eastern milksnake *L. triangulum* is a good proxy for the cryptic ancestral phenotype. They used these morphometric data to make their plasticine replicas of the cryptic and mimetic phenotypes. To make the replicas of the intermediate phenotype, however, they did not have morphometric data on the coastal plains milksnake *L. temporalis*. They, therefore, used the average values of the cryptic and

mimetic phenotypes in each of the 12 morphometric dimensions to create the intermediate phenotype, which luckily resembled the coastal plains milksnake.

To test the probabilities of predator attacks on the three phenotypes, they tied together sets of three replicas, with one of each kind (cryptic, intermediate, and mimetic), so that there was a distance of one meter between each of them. Ten such triads were placed along a transect at a distance of about 75 meters from each other, in the natural habitats of the snakes and their predators. They repeated this experiment with 13 such transects each in Florida (where the model abundance is high) and in North Carolina (where the model abundance is low). All replicas were collected 30–36 days later and, as before, they were scored for predator marks on them by a person unaware of the locations of the replicas.

The results of these experiments were clear-cut. Recall that their hypothesis predicted that in Florida, where the model species is very common, imperfect mimics should be protected even though they are imperfect. As expected, they found that in Florida, the replicas resembling the intermediate phenotype were not attacked any more than the replicas resembling the cryptic and mimetic phenotypes (*Figure* 11, upper panel). Conversely, their hypothesis predicted that in North Carolina, the imperfect mimic should not be protected. As expected again, they found that in North Carolina, the replicas resembling the intermediate phenotype were attacked more than the corresponding rates of attacks on the replicas resembling the cryptic and mimetic phenotypes. In other words, while there indeed was an adaptive valley difficult to cross for the intermediate phenotype in North Carolina, there was no such adaptive valley in Florida. Extending the metaphor of valleys and peaks, we can say that there was a smooth evolutionary landscape in Florida, where the mimic could evolve from being cryptic to be a perfect mimic in spite of having to go through intermediate imperfect phenotypes, perhaps a series of successively improved mimics. Because the intermediate phenotype is protected in Florida, there was no need for one large jump in

Figure 11. Two alternative adaptive landscapes observed in a coral snake Batesian mimicry complex. **(a)** No adaptive valley in Florida where coral snakes are highly abundant models. An a priori contrast showed no difference between the attack rate on the intermediate phenotype versus the attack rate on cryptic and mimetic phenotypes ($Z = 0.01$, $P > 0.9$, $n = 389$). **(b)** Selection against intermediate phenotypes around southern North Carolina where coral snakes are rare. The intermediate phenotype is attacked at a higher rate than cryptic and mimetic phenotypes ($Z = 1.95$, $p = 0.05$, $n = 359$), indicating the presence of an adaptive valley in North Carolina. Asterisk indicates statistical significance.

[Reprinted with permission from: D W Kikuchi and D W Pfennig, High-model abundance may permit the gradual evolution of Batesian mimicry: An experimental test, *Proc. R. Soc. Lond. B*, Vol.277, pp.1041–1048, 2010.]
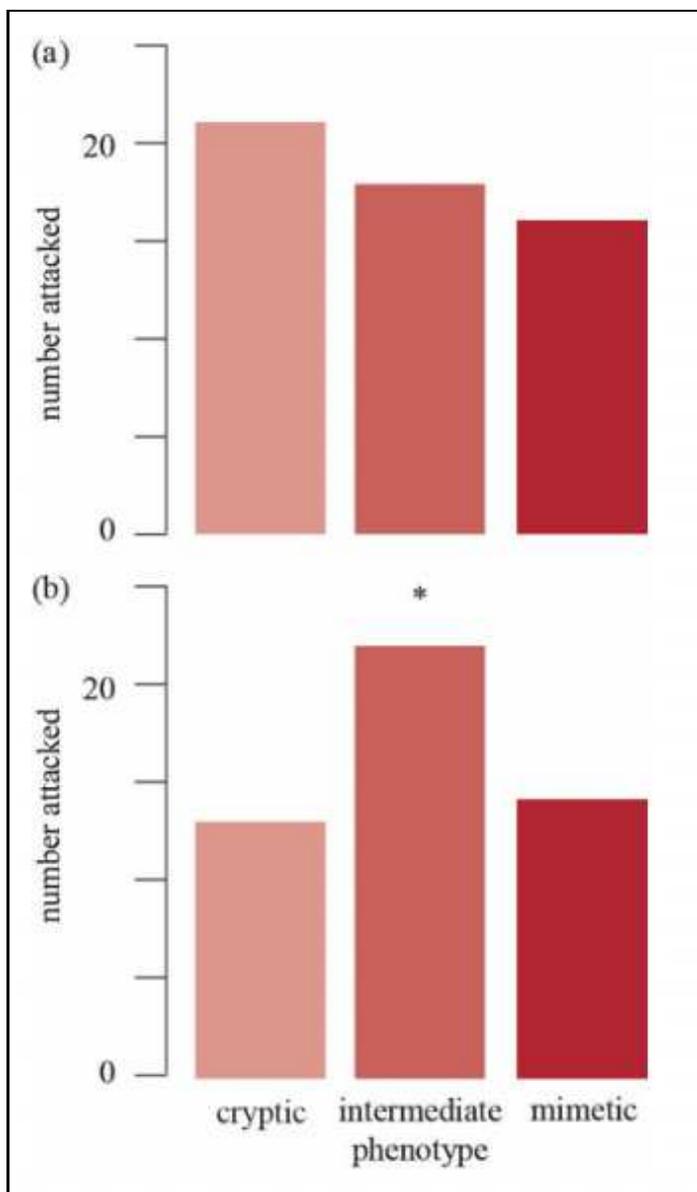
phenotypic space of the kind facilitated by supergenes; gradual changes in phenotype in small steps can lead from crypsis to mimicry. This simple experiment provided a powerful solution to a long-standing problem regarding the evolution of Batesian mimicry by gradual evolution [15]. As early as 1958, Ronald

Fisher had considered aposematism and mimicry as 'the greatest post-Darwinian application of natural selection but it is only really now, after the possibility of the gradual evolution of Batesian mimicry has been confirmed, that we can reaffirm Fisher's claim.

In summary, the three simple experiments described in this article have added much confidence in the hypothesis that the non-venomous kingsnakes are Batesian mimics of the venomous coral snake in North America. In addition, the third experiment added further confidence in the hypothesis of Batesian mimicry by showing that perfect mimics can evolve from cryptic ancestors through a process of gradual natural selection. Unlike the existing theory, these experiments, rather than showing how the mimics could jump over the adaptive valley, showed that there was no valley in the first place, at least in some localities. More generally speaking, these experiments overcome the objection that coral snake mimicry violates some theoretical predictions of Batesian mimicry. But they do so not so much by showing that coral snakes do not violate the predictions, but by showing that some predictions based on mimicry in butterflies are not really valid for coral snakes. Thus, the results of these experiments argue strongly that Batesian mimicry in coral snakes is not a just-so-story.

Imperfect Mimicry and the Limits of Natural Selection

More recent research has uncovered many interesting facts about the evolution of Batesian mimicry in the coral snake mimicry complex. After a long period of high abundance of models and the consequent adaptation of the predators to avoid them, if the models go extinct, there would be continued selection on the mimics to remain close to the appearance of the models at least for a time. This is because the predators who know to avoid the models and those that look like them, are still around. Such selection on the mimics could continue much longer if the ability of the predators to avoid the models has become instinctive. There could even be further selection on the mimics to attain improved resemblance to the now-extinct models because the major attention of

The co-evolution of the models, the mimics and the predators, under different com- binations and densities, and under sympatry and allopatry, consti- tute a rich, and dynamic system for further theoretical and experi- mental investigations.

the predators would now be turned to the mimics (with the models gone), especially the imperfect mimics [16]. The co-evolution of the models, the mimics and the predators, under different combinations and densities, and under sympatry and allopatry, constitute a rich, and dynamic system for further theoretical and experimental investigations. Evidence is also accumulating that, unlike some of the butterfly and other arthropod examples, coral snake mimicry may constitute a much more dynamic, back and forth between mimetic warning colouration and crypsis, rather than a stable evolutionary endpoint [17–19].

Reflections

The experiments described in this article score very high marks on all the criteria that I am trying to espouse and eulogise in this series—simple and clever experiments, the thrill of fieldwork, attention to ecology, a side-project becoming larger than life, working with family and former students, asking fundamental questions and coming up with substantial new findings and solving long-standing problems—and all this, I must emphasise, at a trifling cost. Here I would like to especially dwell on two features of these experiments.

"A Different Kind of Modelling"

The first point concerns the clever use of plasticine models in all the experiments described. This turns out to be such a simple and clever technique, and I would love to see it used even more often. The charming subtitle of this section is borrowed from the title of a fascinating review article entitled "A different kind of ecological modelling: the use of clay model organisms to explore predator-prey interactions in vertebrates" that I have recently come across [20]. In this review article P. W. Bateman and A. K. Wolf from Curtin University and P. A. Fleming from Murdoch University, both in Perth, Australia, have reviewed 143 studies from 1984 to 2015, all using clay or plasticine models. The studies investigated prey morphology, habitat fragmentation, predator behaviour and

social interactions, using artificial models of frogs, salamanders, snakes, lizards, birds (including bird eggs) and mice, to study predation by various species of birds, reptiles and mammals.

The review article shows how much we can do in the field using artificial models of animals, encourages others to do so, and suggests ways of improving the technique. For example, we can add smell to the models, or we can test whether predators can call the experimenters' bluff with repeated exposure. It is not at all obvious beforehand whether predators would learn to ignore the models. There are many examples of super-normal stimuli in the ethological literature showing that animals can easily be fooled into preferring biologically inappropriate objects with exaggerated stimuli over biologically appropriate objects with normal stimuli. Here, therefore, is a rich area for experiments that would not only tell us about the limits of the clay models but even more about the relative roles of different stimuli in the perception of the world by different animals in different contexts. And that can lead to further inquiry about why natural selection has made them so. Opportunities for creating significant new knowledge even with low-cost research are limited only by our imagination.

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Empirically Uninformed Theory versus Field Biology Sans Theory

My second point concerns the healthy interaction between theory and data. Notice that in the previous article in this series [21], we asked why male frogs do not do their best when singing to attract mates and, in this article, we asked why non-venomous snakes do not always do their best in mimicking venomous snakes. The recurring theme is that natural selection does not always produce what we may naïvely consider as a perfect adaptation. The fault is ours, not that of natural selection. How then do we correctly frame our expectations regarding adaptations of animals and plants in nature? Clearly, we need both theory and empirical research, the latter preferably under natural or at least well-defined laboratory conditions. We have to steer between the devil

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of empirically uninformed theory on the one hand, and the deep sea of fieldwork without a sound theoretical foundation on the other. The experiments described here illustrate this particularly well. As you would have noticed, every experiment was carefully designed to test the prediction of a well thought out hypothesis stemming from the theory of Batesian mimicry. And yet, the results of previous experiments influenced the theoretical predictions and the design of the subsequent experiments.

Nowhere is this better illustrated than in the case with the counter-intuitive result that there was a stronger selection to be a good mimic where the model was rare (in North Carolina) but not where the model was common (in Florida). This result led to the abandoning of the theoretical idea that mimicry cannot evolve through a process of gradual natural selection because the putative mimic will encounter and be lost in an adaptive valley when it is midway between being cryptic and mimetic. The counter-intuitive result suggested that there is no need to postulate a super-gene which lets the putative mimic jump from crypsis to mimicry. Instead, it suggested the hypothesis that there may be no adaptive valley in the first place. The next experiment vindicated this hypothesis by showing that predators do not discriminate against imperfect mimics in the high model density areas of Florida. Florida thus provides them with a smooth evolutionary landscape to gradually evolve from cryptic forms to mimetic form via the intermediate stages of imperfect mimicry. More generally speaking, the experiments described here and in the previous article in this series [21] have shown interesting new light on 'imperfections' produced by natural selection, be they less than the most attractive songs or less than the most perfect mimicry. The bottom line, of course, is that these are deemed to be imperfections only because we are ignorant of the underlying ecology during the operation of natural selection.

How do we facilitate a healthy interplay between theory and empirical research? Educating students in both theory and experiment from a very early stage is, of course, very useful and, one might say, even essential. But lessons learned from the best edu-

cation are often laid to waste by the periodic eruption of fashions that promote an unbalanced approach in the pursuit of science. Fashions will inevitably rise and fall, but the problem is compounded by the institutional promotion of one fashion or another in the form of biases in funding, hiring and promotion practices. To overcome this tendency, science managers and policymakers need to display a reasonable amount of modesty and a better appreciation of the history of science.

Fashions will inevitably rise and fall, but the problem is compounded by the institutional promotion of one fashion or another in the form of biases in funding, hiring and promotion practices.

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