

**Concepts and Contentions of Coral Snake Mimicry: A View into the Relationship
Between Model, Mimic, and Dupe**

by

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ABSTRACT OF THE DISSERTATION

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Whether there is mimicry of venomous New World coral snakes by seemingly harmless species of snakes has been a long debated evolutionary subject. For some, this is considered a classic example of Batesian mimicry where the coral snake color pattern serves as a warning signal to predators and is imitated by non-venomous snakes to obtain the putative advantages without being venomous themselves. In many cases of mimicry, including more substantiated examples of Batesian mimicry, the mimic and the model have a clear relationship with each other as well as with their signal receivers. The relationships among coral snakes, on the other hand, is dynamic between themselves and their mimics in ways that have yet to be comprehensively assessed. The existing literature regarding coral snake mimicry presents a divisive stance on whether or not mimicry is actually occurring or if the similar phenotypes that coral snakes and other, non-venomous snakes share are due to environmental factors unrelated to the phenomenon of mimicry. The factors that are analyzed by both those who reject the mimicry hypothesis and those that support the idea that mimicry is occurring in this system include color pattern

function, predatory learning, and biogeographic co-localization between model and mimic. In many cases, snake replica experiments aimed to examine coral snake mimicry have yielded results that have been used to both support and reject mimetic hypotheses, depending on the definition of mimicry being utilized. Herein lies the cause for the disjunction prevalent in coral snake mimicry research: the definition of mimicry is not consistent throughout the scientific community and must be reassessed and agreed upon in order for a comprehensive conclusion to be drawn about New World coral snakes and their potential mimics.

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Table of Contents

ABSTRACT OF THE DISSERTATION	ii
ACKNOWLEDGMENTS	iv
Table of Contents	vi
List of Tables	vii
Introduction.....	1
What is Mimicry?.....	1
Color Patterns of New World Coral Snakes and Their Mimics	3
Development of Ringed Coloration in Snakes.....	5
Methods.....	7
Results.....	8
Evidence Against New World Coral Snake Mimetic Systems	8
Environmental Factors of Color Resemblance: Deflective Effect and Critical Flicker Fusion	9
Effects of Aposematic Coloration and Lethal Prey on Predator Cognition	12
Allopatric Breakdown of Resemblance.....	15
Evidence Supporting New World Coral Snake Mimetic Systems.....	16
Color Banding and Illusionary Effects.....	16
Aposematic Coloration and Innate Avoidance.....	18
Mertensian Mimicry as a Solution to Learned Avoidance.....	22
Mimicry Across Geographic Variation from Sympatry to Allopatry	24
Prospective Considerations for the Definition and Study of Mimicry	29
References.....	32
TABLES	37

List of Tables

1: Forms of Mimicry Hypothesized to Exist in Nature.....	Error! Bookmark not defined.
2: Examples of Color Patterns Observed in Coral Snakes and their Supposed Mimics....	40
3: Literature Results that Support or Reject Mimicry.....	42

Concepts and Contentions of Coral Snake Mimicry: A View into the Relationship Between Model, Mimic, and Dupe

Introduction

What is Mimicry?

Mimicry is an evolutionary phenomenon that has arisen independently in a variety of different organisms. It is considered to occur when a species copies one or more phenotypic traits of another species due to the potential selective advantages these traits incur (Vane-Wright, 1980). Despite this fairly simplistic interpretation of the definition of mimicry, there is often confusion about what conditions must be met in order for an organism to be considered mimetic. In many circumstances, non-mimetic systems, such as masquerading or crypsis (defined below, see also Endler, 1981), are incorrectly labeled as mimicry, as both organisms that exhibit mimicry and organisms that exhibit other forms of resemblance, interspecifically, can all be considered phenotypic imitators. Therefore, how does one distinguish between mimetic and non-mimetic systems?

There are two main differences between mimicry and other interspecific resemblance systems: 1) the method in which each system takes advantage of the environment (i.e. signal production) and 2) the roles of the participants within each system. Crypsis, for instance, results when an organism confuses or removes any physiological signal that may alert another organism to its presence, usually a predator; the most common application of this is through camouflage (Vane-Wright, 1980). Crypsis has two direct participants: the cryptid and the organism receiving the cryptic signal. Mimicry, on the other hand, occurs when an organism produces a signal similar to that of another species which induces a behavioral response from other organisms, which in turn should provide an advantage to

the mimetic organism. Mimicry can therefore be considered a tripartite system because there are three direct participants: the mimic, the model, and the signal receiver, also referred to as the operator or the dupe (Pasteur, 1982). A multitude of additional subdivisions for biological imitation have also been developed in order to distinguish between various categories of mimetic and non-mimetic organisms as laid out in the seminal work of Endler (1981).

Most often, when referring to mimicry, two distinct types of tripartite mimicry systems are considered: Batesian and Mullerian. Batesian mimicry occurs when a harmless or palatable species (the mimic) resembles a harmful or unpalatable species (the model) resulting in avoidance by and protection from a predatory species (the signal receiver). Mullerian mimicry is defined as two or more species or co-mimics, that have similar or varying degrees of unpalatability or harmfulness, which resemble each other resulting in increased protection from the predatory signal receiver (Vane-Wright, 1980; Pasteur, 1982; Mallet & Joron, 1999). These mimetic systems remain the primary and most prominent examples of mimicry in nature. In fact, the general term mimicry is often incorrectly used synonymously with Batesian mimicry.

An issue with mimicry is that not every instance of perceived mimicry can be reliably compartmentalized into these two categories. Researchers focused on the development and evolution of mimicry have described a large variety of different types of mimetic systems, which include Batesian mimicry, Mullerian mimicry, and other types that not only branch off of and refine these two basic forms but expand beyond them as well. Even the names Batesian and Mullerian mimicry have been challenged, by some, in favor of the more descriptive terminology of deceptive and reinforcement mimicry, respectively (Sanchez-

Herrera *et al.*, 1981). These various forms of mimetic systems have been described under an assortment of more specific categories ranging from the interspecific relationship between the participants of the system to the type of signal that is produced by the model and its mimics (Table 1).

Color Patterns of New World Coral Snakes and Their Mimics

The concept of coral snake mimicry has been discussed and debated since Cope (1860) first identified similar color pattern variations between coral snake species and other harmless snake species within certain shared geographic ranges (Dunn, 1954). This observation caused others to seek out the reason for this phenomenon and the mechanisms at play, both physiologically and evolutionarily. Some were quick to call it mimicry, such as Wallace (1867) and Sternfeld (1913). However, others such as Gadow (1908), proposed alternative solutions due to some inherent features of coral snake ecology that were considered contradictory to the process of mimicry development (Dunn, 1954). These features have been discussed by multiple authors and include the high lethality of coral snake venom (Gans, 1961; Huheey, 1980; Brodie III & Brodie Jr, 1999; DuVal *et al.*, 2006), the non-consistent responses by predators when introduced to coral snakes (Livdahl, 1979; Brugger, 1989; Briskie *et al.*, 1992; Beckers *et al.*, 1996; Kikuchi & Pfennig, 2010), and the fact that some supposed mimics do not occur sympatrically with coral snakes (Pfennig *et al.*, 2007; Harper Jr & Pfennig, 2008; Kikuchi & Pfennig, 2009; Pfennig & Mullen, 2010).

In general, the color patterns in coral snakes and their mimics follow a similar theme of colored rings, but each species exhibits different colors, number of rings, and order of rings. Some species look more similar and others look less similar to each other depending on

the mimetic fidelity, or amount of phenotypic similarity, for each of these traits. Homochromy is often incorrectly imagined as a direct one-to-one copy of another species' coloration, but oftentimes this is not the case. In most circumstances, the mimics do not look identical to their models and upon examination could be readily distinguished from one another. Different groups of snakes that share similar body sizes (including length, girth, mouth gape, etc.), environmental conditions, and behavioral attributes tend to share similar color patterns as well. These similarities present an opportunity for mimicry to occur because organisms that share their environment, behavior, and coloration will also benefit in similar ways based on these shared features. Some snakes that exist in more monochromatic locations tend to be uniform in color while other snakes that navigate through a variety of terrain typically exhibit multiple colors (Brattstrom, 1955). Larger and slower snakes most often have blotched patterns with more muted colors like browns, greys, and greens. Snakes that are considered faster, on the other hand, usually have striped and ringed patterns with bright aposematic colors like red, orange, and yellow (Brattstrom, 1955; Pyron & Burbrink, 2009). Venomous coral snakes and their mimics fall into the latter category (Jackson & Franz, 1981). The perceived ancestral form of ringed coloration in snakes is a bi-color pattern where two different colored rings (usually black and red or black and white) alternate along the body of the snake. This two-color pattern is found mostly in non-coral snakes but about forty percent of the specimens with this coloration were found to be coral snakes (Dunn, 1954). A variety of other prominent ringed color morphs found in coral snakes and their imitators have also been characterized for identification (Table 2).

Development of Ringed Coloration in Snakes

The initial development and appearance of the ringed coral snake coloration in other species of snakes remains a majorly disputed area of research due to the relative complexity of the color pattern. One suggestion posits an initial large phenotypic change followed by smaller subsequent changes (Gamberale-Stille *et al.*, 2011). For advocates of mimicry, this hypothesis specifies that a colubrid species of snake that currently displays mimetic phenotypes may have initially undergone a genetic and phenotypic saltation that introduced a coloration pattern similar to a coral snake species, which then led to a relative increase in the colubrid species' fitness, presumably due to the increased resemblance to its dangerous counterpart. Since their fitness improved with this new phenotypic variation, potential selective pressures such as predation, resource competition, or reproductive success induced gradual changes of the colubrid phenotype that converged onto the model phenotype more extensively (Mappes & Alatalo, 1997a; Caley & Schluter, 2003; Kikuchi & Pfennig, 2009). The classic example used to explain this two-step process of genetic saltation, or abrupt large-scale change, and phenotypic gradation in snakes is the suspected evolutionary refinement in color pattern of *Lampropeltis elapsoides*, the scarlet kingsnake. *Lampropeltis elapsoides*, which has a tri-color ringed pattern that closely resembles the coral snake phenotypic coloration of red-yellow-black, is thought to actually have a more cryptic, blotched brown-colored phenotype as its original ancestral morph. Eventually, the genotype and phenotype underwent a saltation to a blotched red coloration and subsequent smaller changes led to the notorious ringed pattern associated with the eastern coral snake, *Micrurus fulvius* (Gamberale-Stille *et al.*, 2011). Evidence for this hypothesis comes from observations of related extant colubrid species that exhibit these ancestral and intermediate color variations, such as the *Lampropeltis triangulum* species complex, which has brown-

blotched as well as red-blotched color patterns within different populations (Gamberale-Stille *et al.*, 2011).

While saltation followed by gradation of color pattern has been a leading concept for the process of mimicry development in harmless snakes, there remain aspects to the genetic causes of these mechanisms that are not entirely understood. What are the specific factors that determine the development of these phenotypes in similar species? Unfortunately, no single answer explains the various instances of color pattern mimicry and their origins are considerably different for snake species than for other organisms, such as invertebrates. The red and black pigmentation that is found in coral snakes and other harmless snake species appear to have differing biochemical structures and distributions within the body, implying that the expression of these pigments is controlled by separate loci that are not linked to each other and could therefore be more readily lost from a population (Rabosky *et al.*, 2016a). This suggests that the coloration found in coral snakes and their mimics has an indirect basis for persisting in nature that is not entirely controlled by the genes for color pigmentation. Coral snakes are unique from other model species such as insects because of the relatively high level of danger associated with interacting with them due to their venom. Therefore, the risk of mistaking a harmless species with a coral snake could be more substantial and the cost of doing so may be fatal. Consequently, it is thought that predators avoid any organism that resembles a coral snake in order to reduce this risk, which then allows for the persistence of the black and red coloration. Even though the pigments are expressed independently of each other, the genes controlling them are positively selected for by predatory avoidance and polymorphisms that are uncharacteristic of a coral snake will be selected against at a faster rate (Caley & Schluter, 2003; Rabosky *et al.*, 2016a).

Even though there are many ideas regarding coral snake mimicry and its development, those who support a mimetic hypothesis do not all agree on the type of mimicry that is occurring or what its driving forces may be. Likewise, those that view these aspects of phenotypic similarity who say that the resemblance does not signify mimicry at all have proposed possible alternative explanations, although these alternatives have not been entirely agreed upon either. Regardless of whether or not mimicry is believed to be the cause of coral snake resemblance in harmless species of snakes the incongruous nature of the interpretation of mimicry by different individuals is one of the biggest challenges facing coral snake mimicry research, which must be resolved in order to produce more robust and cohesive studies in the future.

In this review, we examine one of the most challenging mimetic relationships to understand between New World (NW) coral snakes (*Micrurus* and *Micruroides*) and the snakes that presumably mimic them. In an effort to summarize the history and describe the validity of this system the current body of literature on NW coral snake mimicry will be analyzed to better understand the details and nuances of this complex evolutionary relationship.

Methods

A series of literature searches were conducted using Google Scholar between January 2018 and July 2018, relating to coral snake mimicry and mimetic systems found within other organisms. Keywords and phrases that were utilized in this search included: “Coral Snake Mimicry”, “Batesian Mimicry”, “Mullerian Mimicry”, “Development of Mimicry”, “Mimicry in Allopatry”, “Mimicry in Sympatry”, “Competitive Mimicry”, “Predation on Mimics”, and “Crypsis vs. Mimicry.” Each relevant paper was reviewed and tallied as either supporting coral snake mimicry, refuting coral snake mimicry, or having a neutral

stance on the existence of coral snake mimicry. It is important to note that some of the articles that were tallied as neutral favored explanations that were supportive of mimicry while others favored opposing explanations, although no official stance was made.

Results

From the search results, 58 relevant journal articles were examined within this review (Table 3), with a publication range from 1954 to 2017. Out of the 58 papers being reviewed, 35 (60.3%) were entirely in support of the concept of mimicry in coral snakes, 5 (8.6%) were opposed to mimicry, and 18 (31%) were neutral. Out of the 18 neutral papers, 6 (33.3%) favored a mimetic stance, 1 (5.6%) favored a non-mimetic stance, and the remaining 11 (61%) were entirely neutral. It is clear that articles in support of mimicry as an explanation for phenotypic similarities between coral snakes and other non-venomous snakes are the most prominent. In the earlier stages of mimicry research, there were fairly equal amounts of published studies that either supported, opposed, or were neutral towards mimicry, but, beginning in the 2000s, publications that were neutral or in opposition to mimicry began to dwindle and most articles were in support of it or at the very least held a neutral stance with a favored supportive hypothesis. In reviewing these relatively new articles, a majority of them do not question whether the existence of mimicry is valid; they base their work on the assumption that mimicry is already the answer to try and determine how this system functions in nature.

Evidence Against New World Coral Snake Mimetic Systems

The common argument as to why mimicry should not be considered a viable explanation for the development of similarities between coral and non-coral snakes is that what might

be presumed to be mimicry is actually a convergent force driving evolutionary change between both the model and the mimic that is dependent on extrinsic constraints produced by the environment that the snakes exist in, not a driving force that solely pushes a mimic towards a model's phenotype (Sanchez-Herrera *et al.*, 1981). Such constraints include thermoregulatory requirements, chemical composition of an organism's diet that integrates specific pigmentation, advanced illusionary effects that are components of cryptic coloration, as well as a various assortment of other possibilities that are not traditionally defined as mimicry (Brattstrom, 1955; Pfennig & Mullen, 2010). According to those who do not support mimetic hypotheses, these environmental constraints or the combination of these driving forces are the major factors that determine the mimetic fidelity between organisms that have been observed in nature and not the relationships between model, mimic, and signal receiver.

Environmental Factors of Color Resemblance: Deflective Effect and Critical Flicker Fusion

An analysis of different color pattern data allowed for researchers to discern the relative abundance of certain color morphs within various geographic locations as well as whether or not those morphs belonged to venomous coral snakes or their harmless mimics. It has been shown that as the geographic location of the populations change, the specific color patterns found in the coral snakes and their imitators that are native to those locations changes as well; this holds true regardless of the region being examined (Savage & Slowinski, 1996). One of the more popular notions for this phenotypic similarity is that shared environmental and physiological factors such as light sources, surrounding background environments, thermoregulatory requirements, food availability, and body size might be the primary driving forces for these geographical color resemblances (Wüster *et*

al., 2004; Pryon & Burbrink, 2009). According to this alternative hypothesis, the specific colors that are found on these types of quick moving snakes have developed due to functional requirements such as black bands allowing for better thermoregulatory control (Wüster *et al.*, 2004) or as a consequence of diet such as the red bands developing through the incorporation of carotenoids or other similar pigments that are ingested by the snakes, although this hypothesis is yet to be substantiated by any significant evidence and is only used to explain the coloration but not the ringed patterning (Brattstrom, 1955).

While these coloration hypotheses are plausible and would support rejecting mimicry as the driving factor for similar colorations, the most favored non-mimetic hypothesis is that the ringed patterns of snakes generate an illusionary effect to aid in escape from predators. Similar ringed color patterns found between coral snakes and other non-venomous snakes developed not as a form of mimicry but as an independent method for both groups to avoid and confuse the senses of predators. The illusionary hypothesis was first introduced by Gadow (1911) who stated that "at dusk . . . black, alternating with red produces an effactive blur." Essentially the striped and ringed patterns of snakes create a visual effect that blurs the image of the snake in the eyes of predators when the snake is in motion by obscuring the outline of the snake and their rings, especially when moving on a mottled background such as gravel, rocks, or in grassy areas. When snakes that exhibit stripes or rings move quickly through the environment, a predator that has seen them will view the patterned snake as stationary even though it is not. As a predator looks at the moving striped or ringed pattern of the snake, the illusion, sometimes called the deflective effect, causes their eyes to become fixed at a certain point along the body as the rings become smaller, until the snake is gone and free from danger (Brattstrom, 1955).

The illusion that is generated by ringed patterns on quick moving snakes has also been thought to rely on initial rapid movement followed by sudden motionlessness, as opposed to the deflective effect which only requires quick motion to achieve the illusion. The way this illusionary effect works is through the exploitation of the predator's critical flicker frequency (CFF). The CFF is the rate at which an organism can visualize a light stimulus as if it were steady; similar to how a strobe light that flashes quickly enough will appear to not flash at all. Small, fast snakes with banded patterns have been shown to be capable of moving at a velocity that exceeds the CFF of its predators, creating the illusion of the snake being unicolored while in motion (Pough, 1976; Niskanen & Mappes, 2005). As the ringed pattern moves across a predator's field of vision, the light stimulus generated by the snake's colors are processed more slowly by the eye and the rings on the snake appear to blend together, creating an image of a snake that is monochromatic. The advantage of this relates back to the illusion's reliance on sudden motionlessness, causing the snakes' velocity to fall below the predator's CFF allowing the ringed pattern to be easily visualized. When this type of cessation of movement occurs, the initial unicolored appearing snake would be replaced with a more cryptic ringed pattern in the eyes of the predator, causing the snake to essentially disappear from the predator's view and allowing the ringed snake to escape (Pough, 1976). One interesting example that shows this behavior which corresponds to CFF is with *Nerodia sipedon*, a potential imitator of *M. fulvius*, which only exhibits the representative banding pattern as a juvenile when its body size is capable of exceeding the CFF of its predators (Pough, 1976; Allen, et al. 2013).

Furthermore, there have been hypotheses related to these illusionary effects which state that the red coloration in coral snakes and their mimics adds an extra layer to the illusion

for predators with color vision by breaking up the image of the snake even more when motion ceases. However, for colorblind predators and during the hours of darkness the coloration itself does not provide much of a benefit (Greene & McDiarmid, 2005). During these crepuscular times of day the critical flicker frequency of a predator decreases and banded snakes are more easily able to exceed the CFF and create the blurring illusion; this is further substantiated by the fact that many coral snakes and their imitators are crepuscular in nature (Pough, 1976; Titcomb *et al.*, 2014). Interestingly, it has also been shown that maintaining consistent ring width in snake patterning is an additional important factor in deterring predators (Brodie III & Moore, 1995; Hinman *et al.*, 1997). Alteration of ring size would alter the critical flicker frequency causing the illusion to be less effective, therefore leading to a conservation of ring width in which the illusionary effect is preserved. It is thought that this physical effect might be one of the primary driving forces for the iconic ringed pattern of coral snakes and their supposed mimics, exerting equal pressure on both groups to conform to this advantageous phenotype. If this assumption is correct, mimicry might not be occurring at all because each snake species with this phenotype would be independently converging onto this specific color pattern regardless of the other species. If it were mimicry, the mimetic convergence would be dependent on the phenotype of the model organism, the coral snake.

Effects of Aposematic Coloration and Lethal Prey on Predator Cognition

One phenomenon that has led to the assumption that mimicry is occurring between snakes is that predators have been observed to have a sense of caution and avoidance when interacting with aposematically colored prey (Brodie III & Janzen, 1995; Beckers *et al.*, 1996; Mappes & Alatalo, 1997b). This avoidance is believed to be learned due to the

danger associated with the coral snake just as Batesian and Mullerian mimicry specify. While this hypothesis is an appealing explanation for perpetuated mimicry, there are those that disagree that the avoidance being observed is truly an instinctive response to danger associated coloration. It has been proposed that the aversion is due to the novelty of the stimulus and not necessarily the stimulus itself. This important trait that causes predators to avoid a stimulus that they have never encountered before is the phenomenon known as neophobia (Brodie III & Janzen, 1995; Beckers *et al.*, 1996). If this is in fact the cause of avoidance behaviors, it would mean that these aposematically colored snakes would have converged independently on a ringed color pattern because they both equally benefited from the neophobia that is expressed by their predators. In order to address this oppositional conjecture, experiments using plasticine replicas with dull control colors, coral snake colors, and unnatural pink colorations (Mappes & Alatalo, 1997b). were conducted. The predatory birds used in these experiments, the great tit (*Parus major*), showed avoidance of both the coral snake and the novel pink colorations, garnering support that the ringed pattern of coral snakes acts as a deterrent due to its unfamiliarity (Mappes & Alatalo, 1997b).

Another major issue with the acceptance of learned avoidance as the driving predatory response for mimicry to coral snakes is that coral snake venom is one of the most potent and deadly snake venoms in the world. How is it possible for avian predators to have initially learned of this potentially lethal prey during their lifetimes without succumbing to the deadly venom themselves? Several hypotheses have been suggested to provide a solution to this question, yet none have successfully been supported (Brattstrom, 1955). One of the more prominent hypotheses is that during attacks a bird may not be killed by

the snake venom in circumstances where the venom is not properly injected into the bird especially since the snake would be handled cautiously to begin with. In these situations, it is likely that due to the way the bird is attacking and how the snake struggles while attempting to escape the talons and beak of a flying predator, the strike of the snake would not be as efficient and effective as it would be when acting as a predator itself. The scenarios presented within this hypothesis suggest that it is possible for the snake's fangs to only partially injure the attacking bird with shallow grazes and cuts from its fangs as opposed to a complete puncture wound, resulting in a less than lethal dose of venom injected into the bird (Gans, 1961; DuVal *et al.*, 2006). However, the chances of this type of event occurring enough times for a widespread development of mimicry to occur seems highly unlikely and thus there must be a process that accounts for other, more common, scenarios.

A similar hypothesis discusses the possibility of empathic learning. Empathic learning is when one or more individual predators act as third-party observers of an attack on a dangerous prey item and learn of the associated danger when the primary attacking predator is wounded or killed by the prey (Pough, 1988). In order for this type of learning to be plausible, a few assumptions must be made: 1) predators other than the attacking individual must be present and aware during an attack, 2) the attack itself must result in an observable negative consequence such as injury or death, 3) the predators must be able to recognize the prey item as the cause of the negative consequence, and 4) the predators must be able to remember and subsequently avoid the dangerous prey in the future. There are a few issues with these assumptions as well, such as the fact that an entire population of bird needs to avoid the coral snakes and their mimics in order for mimicry to persist within the

environment. The chances that a majority of these birds, if not all of them, learned to avoid the snakes through secondhand experience is low. Both of these learned avoidance hypotheses share a common issue: there is no plausible situation in which every avian predator that interacts with coral snakes and their mimics is capable of learning to avoid these species to the extent that has been observed in nature through these methods. Therefore, if primary and secondary learning cannot explain this type of predatory behavior, the non-mimetic convergence resulting from neophobia is the best option to explain similar colorations between snakes in regard to predatory avoidance responses.

Allopatric Breakdown of Resemblance

Perhaps one of the most cited arguments against mimicry systems related to coral snakes is the existence of allopatric imitators. Mimicry is thought to only ever occur when the mimic and the model are sympatric to one another, yet there have been instances of supposed coral snake mimics living in allopatry to their proposed model (Brattstrom, 1955; Matthews, 1977; Sweet, 1985; Brugger, 1989; Greene & McDiarmid, 2005; Harper Jr & Pfennig, 2007, 2008; Pfennig *et al.*, 2007; Pfennig & Mullen, 2010; Akcali & Pfennig, 2017). It is thought that allopatric mimicry should never occur because if mimicry is dependent on selective pressures that arise due to the presence of a model, then how would it develop in the absence of a model? The issue here is the fact that mimicry requires the negative association of danger from the models to affect the development of similar phenotypes in the mimic. Since some supposed coral snake mimics exist in allopatry to their proposed models the reinforcement of coral snake coloration shouldn't protect the imitators without the negative effects of the coral snake's venomousness being present.

In order to try and determine how coral snake imitators are able to persist in allopatry, empirical field experiments have been conducted using plasticine replicas in areas where coral snakes and their mimics exist in sympatry as well as areas where they exist in allopatry (Pfennig *et al.*, 2001; Akcali & Pfennig, 2017; Kikuchi & Pfennig, 2009). One such experiment determined that predatory attacks on coral snake and mimetic replicas occurred more often in areas that are allopatric to the native range of coral snakes than in areas of sympatry, showing that as the venomous model decreased in abundance the protection it provided for similarly aposematic colored snakes starts to break down (Pfennig *et al.*, 2001; Akcali & Pfennig, 2017). This lends credence to the idea that mimicry cannot occur in the absence of a model species and therefore there must be an alternative explanation for similar phenotypes between coral snakes and other harmless snake species. However, even though there are hypotheses that reject coral snake mimicry, the fact remains that there are many harmless snakes with coral snake colorations that exist allopatrically with coral snakes. There have been cases of predatory avoidance associated with coral snake recognition and the color patterns that are present in harmless snakes have been shown to correspond greatly to the coral snake species that exist in the same regions. Based on these observations, mimicry has still been the most recognized reason for these similarities despite the previously laid out hypotheses that suggest that it may not be the most reliable explanation.

Evidence Supporting New World Coral Snake Mimetic Systems

Color Banding and Illusionary Effects

Outside of mimicry, color pattern variation between coral snakes and their supposed mimics has been posited to be caused due to environmental constraints such as temperature,

diet, and illusionary effects but there are additional considerations to take into account. Coral snake colorations changes throughout their geographic locations. Interestingly, many of the harmless counterparts that we consider mimics which live sympatrically with each of these coral snake species have color patterns that change with their location as well and that color pattern is seemingly determined by the coloration found in their respective coral snake models, signifying that mimicry is occurring (Savage & Slowinski, 1996). This is supported by intraspecific individuals of harmless snake that have patterns that differ from one another but are each phenotypically similar to the specific coral snake species that it lives with, in sympatry (Savage & Crother, 1989; Greene & McDiarmid, 1981). For example, Gunther's false coral snake, *Erythrolamprus guentheri*, which is found in eastern Ecuador and Peru, has coloration that is extremely similar to the red, black, and white ringed *Micrurus langsdorffi* as well as the black and white ringed *Micrurus margaritiferus* depending on the proximity of the false coral snake to either of the putative model coral snakes (Greene & McDiarmid, 1981). This type of color pattern resemblance is not uncommon and is an important piece of evidence supporting coral snake mimicry systems. How is it known, though, that these associated differences are not due to other factors and are just coincidentally correlated with a mimetic hypothesis?

Experiments were performed in an effort to show that the ringed patterns of supposed coral snake mimics are in fact based on the coral snake models and not on cryptic effects dependent on the environment and the coloration acts instead as a deterrent to predators as exhibited by mimetic systems. Two such experiments were conducted separately in Costa Rica from 1989 to 1990 (Brodie III, 1993) and in Argentina from 2001 to 2002 (Buasso *et al.*, 2006); both experiments used plasticine replicas of coral snakes with classic tri-color

banding patterns of the native species as well as control replicas that were uniformly colored. The replicas were placed in various locations within the native ranges of the coral snakes on natural backgrounds found in the environment, and on white backdrops in order to remove the possibility of the snake blending into the environment. In both circumstances the ring patterned replicas were attacked by wild predators less often than the uniform replicas, indicating that the ringed pattern is aposematic as opposed to cryptic (Brodie III, 1993). What these experiments conclude is that regardless of how visible or concealed the ringed pattern on a snake may be, based on the background that they are viewed on, predators still have preferential avoidance behaviors when compared to more uniform snakes and therefore the driving force for harmless species of snakes to have similar coloration to coral snakes is not due to the cryptic nature that the rings can provide through illusionary effects but due to the aposematic warning coloration that predators associate with the venomous coral snakes providing some substantial evidence to support that mimicry is occurring.

Aposematic Coloration and Innate Avoidance

Along with understanding that ringed snake patterns are aposematic, the most important factor in the development and function of similar coloration is how mimetic species interact with their signal receiver, for this relationship acts as the trigger for evolutionary change. The signal receiver is thought to be any number of various predators, especially avian predators. The laughing falcon (*Herpetotheres cachinnans*) has been shown to be a predator of eastern coral snakes, *Micrurus fulvius*, on more than one occasion. There have been separate accounts of a laughing falcon handling both living and dead Central American coral snakes, *Micrurus nigrocinctus*, as prey (DuVal *et al.*, 2006) and the

stomach contents of other laughing falcon specimens were discovered to contain multiple red colored snakes (Sazima & Augusto, 1991). While it is rare to see any animal confronting a red and black snake there are always exceptions; other birds, occasional large mammals, and some ophiophagous snake species have been shown to prey upon aposematically colored snakes (Dunn, 1954; Livdahl, 1979; Jackson & Franz, 1981; Brodie III, 1993; Beckers *et al.*, 1996). However, a vast majority of researchers prefer to subscribe to the notion that avian species are the primary predators which drive mimicry among snakes.

Wooden and clay snake replicas were used once again and introduced to different naïve birds as a way to test predatory responses and compare them to the aforementioned concept of neophobia. The naïve birds that were used, motmots (*Eumomota superciliosa*) (Smith, 1975) and great kiskadees (*Pitangus sulphuratus*) (Smith, 1977), had no prior exposure to snakes before, let alone snakes with a ringed pattern. During these experiments the naïve chicks had different colored and patterned replicas placed in front of them; some of the replicas were uniformly colored and used as a control to represent harmless snakes and other replicas had the classic red and black ringed patterns of a coral snake. In each case the birds actively avoided the replicas with the coral snake color pattern, but they tended to investigate the uniform replicas. A significant conclusion is that avian predators have developed at some point an innate aversion to these color patterns that are representative of venomous snakes as opposed to neophobia because they investigated the dull colors which were also novel to them. Innate recognition and aversion are important factors for supporting mimicry because it is a reasonable argument for why predators may react to coral snake mimics in the same or similar ways in which it reacts to actual venomous coral

snakes. The avoidance behavior of a particular color pattern would cause that color pattern to flourish in the environment due to the lack of predation on it, while less similar color patterns would be removed from the population and further reinforce the aposematic coral snake pattern.

The deduction of how innate avoidance and neophobia affect aposematic coloration and mimicry evolution has been extrapolated upon with continuous rounds of plasticine replica experiments, originally in a controlled environment like with the motmots and kiskadees but later done in the wild where coral snakes inhabit, and in some cases, where coral snakes are not found naturally (Harper Jr & Pfennig, 2007; Pfennig *et al.*, 2007). For instance, even though the experiment that tested the neophobia hypothesis by using pink colored replicas showed the predatory birds avoiding both the coral snake and the novel pink colorations, there were more observed instances of coral snake avoidance showing that neophobia is an aspect of predatory behavioral responses but it doesn't seem to be the major cause of coral snake pattern avoidance and therefore not a reliable reason for the development of similar colorations between snake species (Mappes & Alatalo, 1997b).

Further experimentation led to the determination of how certain aspects of body morphology and coloration affected predatory response. In one case it was tested to see if adult or juvenile snakes were preyed upon more often than the other by having replicas of varying sizes and coloration, depending on the color differences based on the age of the snake. The results showed that there wasn't discrimination between coloration but rather on size. Therefore, harmless snakes of varying ages may act as mimics of adult coral snakes as long as they equal the specific proportions that need to be met for a proper predatory response (Bittner, 2003). A second experiment was performed that was used to determine

the importance of color and pattern on snakes depending on the dry or rainy season. Predation was seen to increase during the dry season as opposed to the rainy season; this is thought to be due to the scarcity of food during the dry season (Buasso *et al.*, 2006). Another hypothesis states that the scarcity of food could possibly reduce the pigmentation of snakes due to reduced intake of dietary items necessary for pigment production, thus decreasing conspicuousness and increasing the predation rate (Brattstrom, 1955; Buasso *et al.*, 2006). Further evidence that has been provided for the argument that specific proportions of colors are necessary for avoidance behavior in predators was determined through an experiment where the order of the coral snake rings and the proportion of red, black, and white rings were altered on the replicas, showing that color order wasn't the primary determining factor of avoidance which is a reason believed by some for why the harmless mimics are not exact copies of their models. Additionally, this study found that the proportion of black coloration required consistency to produce the same avoidance responses from predators but red and white color proportions could vary and end with the same results, suggesting that the black bands on a coral snake are the most important bands in predator recognition and further evidence for why some mimics are not perfectly identical to the models (Kikuchi & Pfennig, 2010). The coloration and proportions of color and body size were thus deemed important factors for recognition of coral snakes and their mimics.

While these experiments indicate the existence of innate avoidance or neophobia in some bird species, they do not take into account the myriad of other avian and non-avian predators that do not exhibit these behaviors which could be potential threats towards coral snakes and their supposed mimics. There have been documented instances of certain birds

capturing and killing coral snakes, supporting the view that innate recognition and innate avoidance are not ubiquitous and may only account for a small percentage of cases involved in the development of snake mimicry. One such incident was of a red-tailed hawk that was found dead with a dead coral snake caught in its talons (Brugger, 1989). This indicated that the red-tailed hawk did not avoid, nor did it ignore the aposematically colored coral snake and lacked an innate recognition of it, or at the very least its innate recognition did not dissuade it from attacking. When captured, the coral snake bit the hawk and injected its venom into it, killing the hawk and showing that a mistake was made on the predator's part. This mistake caused the traits that made the hawk attack the snake to not be passed on, further showing that predatory responses may cause snakes to become more protected. Similarly, a laughing falcon also captured and killed a coral snake, but the falcon left the snake on a tree branch and returned later to eat it (DuVal *et al.*, 2006). This demonstrated that the falcon may have had innate recognition of the warning coloration of the coral snake and decided to attack anyway, but since the danger was recognized the falcon took a precaution instead of being inadvertently killed like the red-tailed hawk. This interesting behavioral process may indicate a deeper understanding and thought behind a predator's actions when confronted with dangerous prey.

Mertensian Mimicry as a Solution to Learned Avoidance

Innate avoidance in avian predators is popular for explaining the occurrence of mimicry between venomous and non-venomous snakes. However, this hypothesis does not fully consider the way in which it originated. Innate avoidance is suggested to be an evolutionary trait that developed due to predators that were predisposed to avoiding aposematic coloration were able to survive and pass on those avoidance genes to the next generation.

However, as for the predators that do not exhibit innate avoidance, a more general predatory response that leads to mimicry must be investigated to better understand the role predators play in phenotypic resemblance. For these species lacking innate responses, learned avoidance has been suggested as to why avoidance of aposematic coloring is present. Learned avoidance is a process involving a predator encountering a dangerous (in this case venomous) prey item and experiencing the danger that is exhibited by the prey, leading to a response that enables the predator to recognize and avoid potentially dangerous prey in the future (Gans, 1961; Smith, 1975; DuVal *et al.*, 2006).

The idea for learned avoidance surrounding coral snakes and their mimics is that avian predators that attack coral snakes will be exposed to the coral snake venom during the attack, experiencing the consequences of attacking anything that resembles a coral snake again. This process of learning to avoid danger requires two important factors following exposure: recognition and memory. In order for a predator to avoid venomous coral snakes in the future, they must be able to recognize individuals as dangerous through sensory cues like vision, and then must be able to remember the danger associated with venomous prey so that they will not make the same mistake of attacking it again (Smith, 1975). It is likely that neither innate nor learned behaviors are completely responsible for the avoidance patterns that have been observed; instead it may be a combination of the two that contributes to initial behaviors and subsequent incorporation into the genome that evolved alongside the development of mimicry in an arms race between mimic and dupe (Brodie III & Brodie Jr, 1999). However, as stated previously, there have been many arguments against the idea that predators are capable of learning from a lethal model so how is it plausible for coral snake mimicry to still be considered in regard to predatory learning?

One hypothesis that addresses this question is the potential existence of Mertensian mimicry. Mertensian mimicry is a controversial form of mimicry that is described as a harmless species acting as a model for a more harmful species, essentially the opposite of Batesian mimicry. It is thought that coral snakes themselves may actually be mimics of their harmless counterparts and these less venomous species act as the prey that produce the learned response in the avian predators because their bites would not be lethal, while still being painful, and thus be able to generate a more widespread reaction and recognition to the coloration that is exhibited by the various snakes that are avoided (Smith, 1975; Sanchez-Herrera *et al.*, 1981; Marques, 2002). Due to arguments surrounding the validity of the existence of Mertensian mimicry, this hypothesis is not well-supported. Furthermore, Mertensian mimicry does not account for the fact that the harmless species' coloration changes throughout their specific geographic ranges based on their proximity to their proposed models. Regardless of these arguments, the fact remains that there is a driving force causing the continued behavior of avoidance in these avian predators when faced with deadly prey, but a significant amount of neurological and biogeographical research is required before a concrete conclusion can be drawn.

Mimicry Across Geographic Variation from Sympatry to Allopatry

The studies that have analyzed geographic variation indicate a gradual breakdown of mimetic fidelity between supposed mimics and their corresponding coral snake models as the mimics occur further into allopatry with their models. This evident decrease in mimetic resemblance has been cited as a major reason why mimicry is not a plausible explanation for similarities between snake species. Mimicry is thought to not be able to occur in allopatric regions from the model species yet there is a resemblance that exists which

eventually disperses with increasing geographic range. Therefore, this resemblance is often viewed as a phenomenon that is caused by non-mimetic factors such as those that have been previously discussed in this paper. Others, however, see this as more evidence for mimicry since it clearly shows that protection of similarly colored snake species occurs with greater effect in the presence of a model species, thus reinforcing mimetic capability in the harmless species. After determining that allopatric mimic replicas were attacked more often, more studies were performed to determine the attack rates in sympatric and allopatric regions depending on the level of mimetic resemblance. One experiment placed “good” mimetic replicas (replicas that looked more similar to coral snake patterns) and “bad” mimetic replicas (replicas that looked less similar to coral snake patterns) in allopatric regions and determined that good replicas were attacked more often in allopatry (Pfennig *et al.*, 2007). However, in a similar experiment at various sympatric locations from deep sympatry (high abundance of coral snake models) to edge sympatry (low abundance of coral snake models), the results indicated that bad mimics were attacked more often in edge sympatry than they were in deep sympatry (Kikuchi & Pfennig, 2009). The results showed that in sympatric regions, the abundance of the venomous model dictated the level of mimicry found within the system. High model abundance allowed for protection of imperfect and weak mimetic species due to the high cost of mistaking the harmless mimic for the harmful model, while low model abundance caused the protection to decrease and only good mimics persisted in these areas of edge sympatry. In allopatry the protection of mimics begins to break down so that good mimics are attacked due to their aposematic coloration with low cost to the predator because a mistake cannot be made in the absence of the model. Another experiment placed replicas of mimetic snakes from

sympatry, allopatry, and hybrid zones between the two regions into both sympatric and allopatric locations in order to determine if the replicas were attacked more frequently in their native ranges or in foreign ranges (Pfennig *et al.*, 2015). As expected, sympatric type replicas, which are relatively good mimics, were attacked more often outside of sympatry. Allopatric replicas, which are relatively poor mimics due to the breakdown of protection, were attacked more often within sympatry. Hybrid replicas were attacked only in areas of edge sympatry where good mimics are favored, but the hybrids persisted more in allopatric regions, which is evidence for why coral snake mimicry may persist in regions where coral snakes do not exist (Mallet *et al.*, 1998; Jiggins *et al.*, 2001).

While the type of protective mimicry being discussed has been determined to develop due to selective pressure from the signal receiver, why are there still mimetic organisms that have not converged entirely onto the phenotype of the model, thus allowing for the continued division between “good” and “bad” mimics? In fact, the majority of observed mimics are considered to be imperfect mimics (Chittka & Osorio, 2007; Kikuchi & Pfennig, 2010, 2013; Pfennig & Kikuchi, 2012; Akcali & Pfennig, 2017). Furthermore, if greater mimetic fidelity is driven by the signal receivers, why is there still an abundance of imperfect mimics found in nature? What conditions exist that prevent complete mimetic convergence? The most obvious answer is that while it may be true that interactions between the mimic and the signal receiver are a major factor in mimetic development it is important to account for interactions with the third participant in the tripartite system, the model. It has been suggested that as resemblance between a mimic and a model increases, competition between the two increases as well, causing an evolutionary shift from high mimetic fidelity to low mimetic fidelity (Pfennig & Kikuchi, 2012). For instance, in order

for the mimetic fidelity of a coral snake mimic such as *L. elapsoides* to approach a high degree of phenotypic resemblance with *M. fulvius* they must not only be similar in coloration and pattern but also in size, feeding patterns, and defensive behavior (Marques, 2002). Organisms that are phenotypically similar tend to inhabit the same niche space due to physiological and ecological constraints placed on them, thus diverging from each other through the process of character displacement (Moynihan, 1968). There appears to be a balance of mimicry that occurs that oscillates between increased mimetic resemblance and decreased mimetic resemblance that corresponds directly with the degree of predatory interactions with the signal receiver and the degree of niche competition with the model, respectively (Pfennig & Kikuchi, 2012)

There have been various hypotheses that explain the persistence of “good” mimics in edge sympatry, and imperfect mimics in deep sympatry. For deep sympatry, some popular hypotheses include how there may be multiple predators that react to different aspects of imperfect coral snake mimics, there may be multiple models that the mimics are copying, models may evolve away from the mimetic phenotype to increase their own fitness, or mimics may have weak selective pressures driving them towards perfect mimicry due to the wide umbrella of protection provided for them by the relatively large number of models in deep sympatry (Yanosky & Chani, 1988; Caley & Schluter, 2003; Pfennig *et al.*, 2007; Kikuchi & Pfennig, 2010, 2013). Alternatively, in edge sympatry, where model abundance is relatively low, there would be a decreased rate of evolution of the model away from the mimetic phenotype and less protection would be provided by the existing models, resulting in strong selective pressures that drive mimics towards a more perfect mimetic resemblance (Harper Jr & Pfennig, 2007; Kikuchi & Pfennig, 2009) In reality, it is likely that all of these

explanations are occurring to some extent and they each act as the direct causes for mimetic variation from deep sympatry to edge sympatry.

Since the level of mimicry within a system is dependent on the density of the model within a geographic range (Matthews, 1977; Livdahl, 1979; Huheey, 1980; Pfennig *et al.*, 2007; Kikuchi & Pfennig, 2009), the question remains, how exactly do mimics persist in locations where there are no models? (Joron, 2008; Akcali & Pfennig, 2014). Three different plasticine coral snake replicas of varying degrees of mimetic coloration were placed in multiple locations allopatric to actual coral snakes. The results determined that replicas that were more phenotypically similar to coral snake coloration were attacked more often by predators than the less similar counterparts, possibly due to the bright aposematic coloration. This suggests that unlike sympatric mimics, greater mimetic fidelity is selected against and mimicry should gradually break down as populations move further into allopatry (Pfennig *et al.*, 2007). However, the rate of mimicry loss is variable and dependent on an assortment of factors. Three processes have been recognized as a means for the maintained presence of allopatric mimics: 1) selection for mimetic phenotypes in allopatry, 2) range contraction of a model species so that allopatric mimics persist, and 3) range expansion of a mimetic species and gene flow from sympatry to allopatry (Pfennig & Mullen, 2010).

Selection for allopatric mimics would be caused primarily by predator cognition. As stated previously, predators have displayed a means of risk management when dealing with mimetic species by avoiding any brightly colored organisms regardless of their prior knowledge of its harmfulness; this includes innate color pattern avoidance as demonstrated by motmots and kiskadees (Smith, 1977; Schuler & Hesse, 1985) as well as avoidance of

any novel specimen (Beckers *et al.*, 1996). There is also possible selection from predators that are sympatric to both the allopatric model and mimic species so avoidance, in these cases, would be learned, resulting in similar selective pressures to those found between sympatric models and mimics (Pfennig & Mullen, 2010). An alternative to basic selection pressures is the hypothesis of range contraction. This refers to the possibility that the model and the mimic were once sympatric until the model went locally extinct and the mimic became partially allopatric to the model. It is thought that there might be a type of “evolutionary momentum” generated from the model before extirpation, which allowed for increased resemblance and greater protection for the model after extirpation (Akcali & Pfennig, 2014). Another possibility is range expansion and gene flow, where mimics from sympatry may migrate into regions without models and introduce the mimetic genes into these allopatric regions, essentially providing a continuous supply of mimetic gene flow into a region where mimicry should not occur, thus preventing its breakdown (Harper Jr & Pfennig, 2008). As with sympatry, the pressures and processes that occur in allopatry all play a role in the continued existence of mimicry, though it is still uncertain which of these hypotheses are the most relevant.

Prospective Considerations for the Definition and Study of Mimicry

The discrepancies between explanations for mimetic hypotheses are widespread throughout each of the areas of research that have been discussed in this review. It is difficult to determine a single conclusive answer to the existence and validity of mimicry between harmless snakes and coral snakes. Each experiment and hypothesis that has been laid out does not provide enough evidence to wholly support or reject mimicry or take into account that multiple factors can be influencing or driving color patterns in these snakes,

working independently or synergistically. The issue with determining mimicry as the actual process behind phenotypic resemblances between coral snakes and their “imitators” also lies within the question of its definition. The experiments that have been performed agree that some harmless snakes share a phenotypic resemblance to coral snakes due to selective pressure. Whether or not the result of this selective pressure should be considered mimicry is the true debate. Some view mimicry as one species benefiting from imitating another species by gaining protection from predation and competition through warning signals, excluding any other environmental benefits such as thermoregulatory control or illusionary effects that simulate crypsis. Others might broadly view mimicry as the imitation of another species that results in any sort of benefit that increases fitness with increasing resemblance. Greater complications in either of these scenarios begin to occur when factors such as extreme danger and lethality, as well as mimic/model allopatric localization, are included within the mimetic system. These situations have always been considered contrary to the perpetuation of mimicry and make it difficult for researchers to describe these systems in the context of an already divided definition of mimicry. However, as research has continued, there has been a shift in discussion surrounding mimicry by the community. Prior to the new millennium, studies pertaining to coral snake mimicry typically expressed indecision or occasionally outright rejection of mimicry as the cause for phenotypic resemblance. This uncertainty seemingly dissipated in the 21st century and was instead replaced by an acceptance of coral snake mimicry with some stances maintaining neutrality but having an overall disposition in favor of mimetic systems. This trend may suggest that the community as a whole realized that mimicry was the answer to these long-debated issues, and oppositional studies were no longer necessary. However, while there is a

modern concession that mimicry is occurring with respect to coral snakes, the processes behind its occurrence are not entirely agreed upon as its definition varies from study to study. There still has yet to be a consensus that mimicry occurs, and by ignoring the arguments that have been made against it, without first determining the extent of mimicry's role as it pertains to coral snakes, any conclusion made might not be the most accurate or complete explanation for the processes that are occurring.

Without a unifying meaning for mimicry and a cohesive understanding of the processes that maintain it in nature, a variety of conclusions could be made that may be unsupported by other definitions of mimicry, further perpetuating the discourse that is inherent in coral snake mimicry. It is necessary to examine how mimicry is defined and expand on those definitions in order to understand the processes driving the phenotypic similarities between snakes and between other organisms as well. Perhaps these resemblances are caused by environmental factors independent of predation; perhaps the so-called model species is diverging from its supposed mimic due to competition. Should these circumstances factor into a new definition of mimicry? Should they be considered something that works in conjunction with mimicry? Coral snake mimicry is fairly unique, mainly due to the lethality of coral snakes, and could be better understood if the processes were considered more as a unification of environmental events as opposed to only mimicry or non-mimicry. The complexity of mimicry systems should not be understated. It is important to realize that mimicry, like any evolutionary process, is dynamic--and by attempting to understand its expression as an amalgamation of many different forces in nature, the study of evolution itself becomes more apprehensible.

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TABLES

Table 1. Forms of Mimicry Hypothesized to Exist in Nature

Major Categories of Mimicry (Smith, 1975; Vane-Wright, 1980; Sanchez-Herrera *et al.*, 1981; Pasteur, 1982; Mallet & Joron, 1999)

Batesian (deceptive)	Harmful model, harmless mimic
Mullerian (reinforcement)	Two co-mimics (each act as model and mimic for the other)
Mertensian (Emslyan)	Harmless model, harmful mimic

Forms of Mimetic Expression (Pough, 1988)

Concrete	Single direct resemblance between model and mimic (ex. Body of mimic looks like body of model)
Abstract	Complex similarities between one or more interspecific taxa (ex. Wing of mimic looks like eye of model)

Tripartite Relationships (Rainey & Grether, 2007)

Disjunct	Model, mimic, and dupe belong to three different species
Bipolar	Two of the three groups belong to one species
Intraspecific	All three groups belong to one species

Types of Mimetic Interactions (Pasteur, 1982; Rainey & Grether, 2007)

Aggressive	Predators/parasites avoid detection by their prey by mimicking harmless models
Reproductive (sexual)	Individuals mimic opposite sex to increase chance of mating and decrease mate competition
Mutualistic	Model and Mimic benefit from mimicry (usually associated with Mullerian mimicry)
Commensalism	One party (usually the mimic) benefits from mimicry without hindering the other

Protective (defensive)	Prey avoids predation by mimicking harmful model (subset of Batesian)
Competitive	Mimic and model compete for resources (food, territory, mates, nesting sites)

Signals sent to the signal receiver (Rainey & Grether, 2007)

Synergic	The mimetic signal is beneficial to the model
Antergic	The mimetic signal is detrimental to the model
Warning	Signal that makes the signal receiver respond negatively to both model and mimic
Aggressive	Signal that makes the signal receiver respond positively to the model and negatively to the mimic
Defensive	Signal that makes the signal receiver respond negatively to the model and positively to the mimic
Inviting	Signal that makes the signal receiver respond positively to both model and mimic

Signals copied from the model (Pasteur, 1982)

Homochromy	Mimicry of visual signals
Homochemistry	Mimicry of chemical signals
Homoelectry	Mimicry of electrical signals
Homophony	Mimicry of auditory signals
Homothermy	Mimicry of tactile signals
Homotopy	Mimicry of one or more of these signals

Other forms of resemblance (Grobman, 1978; Pough, 1988; Mallet & Joron, 1999)

Dual Mimicry	Mimicry of two different models
Quasi-Batesian Mimicry	Parasitic form of Mullerian mimicry due to unbalanced palatability between co-mimics

Pseudo-Mimicry

Not actually mimicry but phenotypic
resemblance driven by pressures
outside of signal receivers

Table 2. Examples of Color Patterns Observed in Coral Snakes and their Supposed Mimics

Non-Venomous Snakes	Coral Snakes
Bi-color (L-B-L)	
<i>Anilius scytale</i>	<i>Micrurus limbatus</i>
<i>Dipsas brevifacies</i>	<i>Micrurus multifasciatus</i>
<i>Lampropeltis getula</i>	<i>Micrurus multiscutatus</i>
<i>Sibon annulatus</i>	<i>Micrurus psyches</i>
<i>Tropidodipsas annulifera</i>	<i>Micrurus ruatanus</i>
<i>Pliocercus euryzona</i>	<i>Micrurus stewarti</i>
Tri-Color Monad (R-L-B-L-R)	
<i>Erythrolamprus mimus</i>	<i>Micrurus alleni</i>
<i>Erythrolamprus pseudocorallus</i>	<i>Micrurus averyi</i>
<i>Rhinobothryum bovallii</i>	<i>Micrurus browni</i>
<i>Scaphiodontophis venustissimus</i>	<i>Micrurus clarki</i>
<i>Sibon anthrocops</i>	<i>Micrurus coarallinus</i>
<i>Pliocercus elapsoides</i>	<i>Micrurus distans</i>
	<i>Micrurus dumerilli</i>
	<i>Micrurus fulvius</i>
	<i>Micrurus nebularis</i>
	<i>Micrurus nigrocinctus</i>
	<i>Micrurus peruvianus</i>
	<i>Micrurus proximans</i>
Tri-Color Dyad (R-B-L-B-R)	
<i>Attractus latifrons</i>	
<i>Cemophora coccinea</i>	
<i>Erythrolamprus aesculapii</i>	
<i>Erythrolamprus bizona</i>	
<i>Lampropeltis pyromelana</i>	

Lampropeltis Triangulum

Lampropeltis zonata

Tantilla supracincta

Tri-Color Triad (R-B-L-B-L-B-R)

Oxyrhopus melanogenys

Micrurus decoratus

Oxyrhopus trigeminus

Micrurus dissoleucus

Micrurus filiformis

Micrurus frontalis

Micrurus hemprichii

Micrurus ibiboboca

Micrurus isozonus

Micrurus laticollaris

Micrurus lemniscatus

Micrurus sangilensis

Micrurus spixii

Micrurus surinamensis

Micrurus tschudii

Tri-Color Pentads (R-B-L-B-L-B-L-B-L-B-R)

Simophis rhinostoma

Micrurus elegans

Table 3. Literature Results that Support or Reject Mimicry

Title	Author(s)	Year
Hypotheses that Oppose Mimicry		
The Coral Snake “Mimic” Problem and Protective Coloration	Brattstrom, B.H.	1955
Multiple Cryptic Effects of Cross-banded and Ringed Patterns of Snakes	Pough, F. H.	1976
Studies in Warning Coloration and Mimicry VIII. Further Evidence for a Frequency Dependent Model of Predation	Huheey, J. E	1980
Coral Snake Mimicry: Live Snakes Not Avoided by a Mammalian Predator	Beckers, G.J.L, et al.	1996
Polymorphic Clay Models of <i>Thamnophis Sirtalis</i> Suggest Patterns of Avian Predation	Bittner, T. D	2003
Hypotheses That Support Mimicry		
Coral-Snake Pattern Recognition and Stimulus Generalization by Naïve Great Kiskadees (Aves: Tyrannidae)	Smith, S.M	1977
An Overview of the Relationship Between Mimicry and Crypsis	Endler, J. A	1981
Coral Snake Mimicry: Does it Occur	Greene, H. & McDiarmid, R.	1981
Another Suggested Case of Ophidian Deceptive Mimicry	Sanchez-Herrera, O; et al.	1981
A Classifactory Review of Mimicry Systems	Pasteur, G.	1982
On the Function of Warning Coloration: A Black and Yellow Pattern Inhibits Prey-Attack by Naïve Domestic Chicks	Schuler, W. & Hesse, E.	1985
Possible Dual Mimicry of Bothrops and Micrurus by the Colubrid, <i>Lystrophis dorbignyi</i>	Yanosky, A.A. & Chani, J. M	1988
The Status of Pliocercus and Urotheca (Serpentes: Colubridae), with a Review of Included Species	Savage, J. M. & Crother, B. I.	1989

Of Coral Snake Mimics

The Colouration of the Venomous Coral Snakes (Family Elapidae) and their Mimics (Families Aniliidae and Colubridae)	Savage, J. M. & Slowinski, J. B.	1992
Frequency Dependent Batesian Mimicry	Pfennig, D. W; et al.	2001
Natural History of the Coral Snake <i>Micrurus decorates</i> (Elapidae) from the Atlantic Forest in Southeast Brazil, with Comments on Possible Mimicry	Marques, O. A. V.	2002
Predators Favour Mimicry in a Tropical Reef Fish	Caley, M. J. & Schluter, D.	2003
Do Aposematism and Batesian Mimicry Require Bright Colours? A Test, Using European Viper Markings	Wuster, W. et al.	2004
Wallace and Savage: Heroes, Theories, and Venomous Snake Mimicry	Greene, H. W. & McDiarmid, R.W.	2005
A Case of Suspected Coral Snake (<i>Hemibungarus calligaster</i>) Mimicry by Lepidoptern Larvae (Bracca sp.) From Luzon Island, Philippines	Brown, R. M.	2006
Predation on Snakes of Argentina: Effects of Coloration and Ring Pattern on Coral and False Coral Snakes	Buasso, C. M et al.	2006
Evidence for a Mullerian Mimetic Radiation in Asian Pitvipers	Sanders, K. L. et al.	2006
Mimicry on the Edge: Why do Mimics Vary in Resemblance to their Model in Different Parts of their Geographical Range	Harper Jr., G. R. & Pfennig, D. W.	2007
Population Differences in Predation on Batesian Mimics in Allopatry with their Model: Selection Against Mimics is Strongest when they are Common	Pfennig, D. W. et al	2007
Selection Overrides Gene Flow to Break Down Maladaptive Mimicry	Harper Jr., G. R. & Pfennig, D. W.	2008
Batesian Mimicry: Can a Leopard Change Its	Joron, M.	2008

Spots-and Get them Back?

High-Model Abundance May Permit the Gradual Evolution of Batesian Mimicry: An Experimental Test	Kikuchi, D. W. & Pfennig, D. W.	2009
Body Size as a Primary Determinant of Ecomorphological Diversification and the Evolution of Mimicry in the Lampropeltine Snakes (Serpentes: Colubridae)	Pryon, R. A. & Burbrink, F. T.	2009
Predator Cognition Permits Imperfect Coral Snake Mimicry	Kikuchi, D. W. & Pfennig, D. W.	2010
Feature Saltation and the Evolution of Mimicry	Gamberale-Stille, G. et al	2011
Competition and the Evolution of Imperfect Mimicry	Pfennig, D. W. & Kikuchi, D. W.	2012
Imperfect Mimicry and the Limits of Natural Selection	Kikuchi, D. W. & Pfennig, D. W.	2013
Rapid Evolution of Mimicry Following Local Model Extinction	Akcali, C. K. & Pfennig, D. W.	2014
More than Mimicry? Evaluating the Scope for Flicker fusion as a defensive strategy in coral snake mimics	Titcomb, G. C. et al.	2014
Batesian Mimicry Promotes Pre- and Postmating Isolation in a snake Mimicry Complex	Pfennig, D. W. et al.	2015
To Mimicry and Back Again	Pfennig, D. W.	2016
Coral Snakes Predict the Evolution of Mimicry Across New World Snakes	Rabosky, A. R. D. et al.	2016
Unlinked Mendelian Inheritance of Red and Black Pigmentation in Snakes: Implications for Batesian Mimicry	Rabosky, A. R. D. et al	2016
Geographic Variation in Mimetic Precision Among Different Species of Coral Snake Mimics	Akcali, C. K. & Pfennig, D. W.	2017
Selective Advantage Conferred by Resemblance of Aposematic Mimics to Venomous Models	França, F. G. et al	2017

Neutral Mimetic Hypotheses

The Coral Snake 'Mimic' Problem in Panama	Dunn, E. R.	1954
Mimicry in Procryptically Colored Snakes of the Genus <i>Dasypeltis</i>	Gans, C.	1961
Innate Recognition of Coral Snake Pattern by a Possible Avian Predator	Smith, S. M.	1975
An Alternative Solution to the Coral Snake Mimic Problem (Reptilia, Serpentes, Elapidae)	Grobman, A. B.	1978
Ecology of the Eastern Coral Snake (<i>Micrurus fulvius</i>) in Northern Peninsular Florida	Jackson, D. R. & Franz, R.	1981
Mimicry of Vertebrates: Are the Rules Different?	Pough, F. H.	1988
Red-Tailed Hawk Dies with Coral Snake in Talons	Brugger, K. E.	1989
Habits of Five Brazilian Snakes with Coral-Snake Pattern, Including a Summary of Defensive Tactics	Sazima, I & Augusto, S. A.	1991
Differential Avoidance of Coral Snake Banded Patterns by Free-Ranging Avian Predators in Costa Rica	Brodie III, E. D.	1993
Experimental Studies of Coral Snake Mimicry: Generalized Avoidance of Ringed Snake Patterns by Free- Ranging Avian Predators	Brodie III, E. D. & Janzen, F. J.	1995
Experimental Studies of Coral Snake Mimicry: Do Snakes Mimic Millipedes?	Brodie III, E. D. & Moore, A. J.	1995
Evolution of Coloration, Urotomy, and Coral Snake Mimicry in the Snake Genus <i>Scaphiodontophis</i> (Serpentes: Colubridae)	Savage, J. M. & Slowinski, J. B.	1996
Predation by Free-Ranging Birds on Partial Coral Snake Mimics: The importance of Ring Width and Color	Hinman, K. E. et al	1997
Predator-Prey Arms Races Asymmetrical Selection on Predators and Prey May be Reduced when Prey are Dangerous	Brodie III, E. D. & Brodie Jr., E. D.	1999

Significance of the Dorsal Zigzag Pattern of <i>Vipera latarsei gaditana</i> Against Avian Predators	Niskanen, M. & Mappes, J	2005
Laughing Falcon (<i>Herpetotheres cachinnans</i>) Predation on Coral Snakes (<i>Micrurus nigrocinctus</i>)	DuVal, E. H. et al.	2006
Responses of Greater Roadrunners During Attacks on Sympatric Venomous and Nonvenomous Snakes	Sherbrooke, W. C. & Westphal, M. F.	2006
Mimics Without Models: Causes and Consequences of Allopatry in Batesian Mimicry Complexes	Pfennig, D. W. & Mullen, S. P.	2010
