Spring 4-30-2021

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Recommended Citation
Hendricks, Matt, "An Examination of Mimetic Precision and the Selective Advantages of Imprecise Mimics" (2021). *Honors Theses*. 1906.
https://egrove.olemiss.edu/hon_thesis/1906

AN EXAMINATION OF MIMETIC PRECISION AND THE SELECTIVE ADVANTAGES OF IMPRECISE MIMICS

By
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A thesis submitted to the faculty of The University of Mississippi in partial fulfillment of the requirements of the Sally McDonnell Barksdale Honors College.

Oxford, MS
May 2021

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DEDICATION

To Jim and Amy, for their ceaseless love and support. I thank them for the sacrifices which they have made to provide me with a life full of opportunity. I am truly blessed to have them as parents.

ACKNOWLEDGEMENTS

Thank you to Dr. Brice Noonan and Dr. Renan Janke Bosque, for providing me with the opportunity to get involved in research as an undergraduate and for being a tremendous help to me while I was completing this project. Additionally, a big thanks to Dr. Susan Balenger and Dr. Christopher Leary for serving on my thesis committee.

I thank the many friends, family members, and university faculty who have been supportive of me during this process and throughout my four years as an undergraduate at the University of Mississippi. I am blessed to have gained such a supportive and extensive network of people while an undergraduate. Additionally, special thanks to Adriana Jones, who committed a lot of her time and energy assisting in every single step of this project.

Next, I thank the Honors College faculty and staff for providing me with the fantastic facility and learning environment that I have greatly enjoyed throughout the last four years. I am incredibly grateful to have been involved with the Honors College during my college experience.

Finally, I would like to thank Tim, Rachel, and Katya of Florida State University for assisting in the data collection phase of this project.

ABSTRACT

MATTHEW ROBERT HENDRICKS: An Examination of Mimetic Precision and the Selective Advantages of Imprecise Mimics (Under the direction of Brice Noonan)

First proposed by Henry Walter Bates in 1862, Batesian mimicry refers to the scenario in which an undefended species (the mimic) gains protection from predation due to its phenotypic resemblance to a noxious species (the model). Often, the model species possess a conspicuous phenotype which serves to warn predators of the species' danger. A great deal of research spanning many decades has been devoted to this phenomenon as it applies to coral snakes. Coral snakes are quite noxious and are distinguished from other species of snakes by their banded patterns of bright colors such as red, yellow, and black. It is often observed in nature that the degree to which mimic species resemble their models is quite variable according to geographic location and levels of model abundance. In other words, many "imprecise" mimics exist in nature, across many taxa. This phenomenon holds true for coral snakes and their mimics. For example, certain species of the snake genus *Oxyrhopus* (the mimics) in South America possess shifted (left/right misalignment of bands) patterns which are not found on species of the genus *Micrurus* (their models). In order to assess the selective forces acting on imprecise mimics of coral snakes, we constructed clay replicas of three different phenotypes (840 replicas total). These replicas were deployed in Florida's Apalachicola National Forest in order to sample predation rates on each variant. Two of the phenotypic variants served as imprecise mimics, possessing shifted patterns analogous to those of species of *Oxyrhopus*, while the third variant served as a precise mimic, possessing no shifting. The predation rates on each of the model variants did not differ, indicating that in areas where a defended model exists there is not a selective disadvantage experienced by imprecise mimics of coral snakes, specifically those possessing shifted patterns.

TABLE OF CONTENTS

LIST OF FIGURES

INTRODUCTION

Often in nature, conspicuous phenotypes or color combinations such as red, yellow, and black serve to warn predators of the danger which might befall them if they choose to attack a potential prey species (Wallace 1889). Species which possess these conspicuous patterns/colors and are dangerous or unprofitable to potential predators are referred to as aposematic, a term first coined by Edward Bagnall Poulton (Poulton 1890). Aposematic species are often equipped with secondary defenses (toxins and venoms) transmitting in this sense, an honest signal of danger to potential predators. Predators, through experiential learning or innate sense, choose to avoid aposematic species due to the risk they pose. Often, the signals used by aposematic species, such as bright coloration, are co-opted by species without secondary defenses. These species may be described as “undefended.” The exhibition of another species’ aposematic signal(s) by an undefended species results in the deception of predators. Predators mistakenly identify the undefended species as a defended species which they choose to avoid, providing for the protection of the undefended species. The phenomenon of different species sharing similar signals that are targeted to the same receivers (predators) is referred as mimicry.

One example of mimicry that has been widely documented involves coral snakes. These species are distributed across the Southeastern United States, parts of Central America, and throughout South America, where there is a particularly high species richness (Rabosky et al. 2016). Coral snakes have an extremely toxic venom (Cecchini et al. 2005; Delazeri de Carvalho et al. 2014) and they advertise how dangerous they are by colored banding patterns (Figure 1).

Through evolutionary change, the warning coloration of these venomous species has been mimicked by many harmless snake species (Figure 1). Appearing similar to these venomous coral snakes provides undefended snakes with protection from predators. One such species in the southeastern US is *Lampropeltis elapsoides*, commonly known as the scarlet king snake. This snake is harmless yet, due to its phenotypic similarity to the eastern coral snake (*Micrurus fulvius*), it is often avoided by predators. (Pfennig et al. 2001). Two more examples of defended aposematic species are the Brazilian short-tailed coral snake (*Micrurus brasiliensis*) and the southern coral snake (*Micrurus frontalis*). These snakes serve as the models for undefended species of snakes within the genus: *Oxyrhopus*, such *as O. guibei* and *O. trigeminus* (Wallace 1867; Bosque et al. 2015).

. **Figure 1: Photographs of Various Species of Coral Snakes and their Mimics.** *A. Micrurus brasiliensis* (Photograph: NJ Silva Jr.). B. *M. fulvius* (Photograph: Kenneth P. Wray). C. *Oxyrhopus trigeminus* (Photograph: IJ Tomial). D. *Lampropeltis elapsoides* (Photograph: Kenneth P. Wray). E. *O. guibei* (Photograph: NJ Silva Jr.). F. *M. frontalis* (Photograph; NJ Silva Jr.). Shifted patterns are observed in photographs *C.* and *E.*

Coral snakes and their mimic species engage in Batesian mimicry, not to be confused with Müllerian mimicry, the phenomenon describing the mutual benefits received by two defended species that have acquired a similar phenotype through evolution (Müller 1879). Named after Henry Walter Bates, an English naturalist who studied such species relationships within butterflies, Batesian mimicry refers to the process by which an undefended species (the mimic) acquires similar attributes to a defended species (the model) through evolutionary change, due to the protective advantages gained (Bates, H.W. 1862).

The Batesian mimicry complex associated with coral snakes has been studied extensively in the southeastern US (Pfennig et al. 2007; Harper et al. 2007; Ackali et al. 2017) and Central America (Brodie et al. 1993; Brodie et al. 1995). In Brodie et al. (1993; 1995) and Pfennig et al. (2007) an experimental design in which hand-constructed clay replicas of coral snakes and their mimics were deployed in the field was used to investigate predator avoidance. The work of Brodie et al. (1993) in Costa Rica suggests that the banding patterns of coral snakes trigger avoidance amongst predators such as birds (Brodie et al. 1993). Brodie et al. (1993) suggest that this avoidance may be a result of evolutionary change stemming from ancestral knowledge or the experience of individual predators themselves (1995). Harper et al. (2007) have demonstrated that the undefended scarlet king snake is found in both allopatry and in sympatry to its model, the highly noxious eastern coral snake, in North Carolina and Florida. Harper et al. (2007) noted in these studies that, depending on the model abundance in a given geographical location, the resemblance of mimics to their models may vary. Specifically, in areas of lower model (*Micrurus fulvius*) density, mimic species' (*Lampropeltis elapsoides*) resemblance was more precise. In contrast, within areas of relatively high model density, the resemblance of the mimic species is often less precise (Harper et al. 2007). One might reasonably expect that imprecise mimics are less protected from predators resulting in a selective disadvantage of poor mimics. However, these “imprecise” mimics, are commonly found in nature (Dittrich et al. 1993) contrary to what might be expected (Edmunds, 2000; Pfennig et al. 2012).

Imprecise mimics can be found in distant related taxa and are not restricted to coral snakes. Edmunds (2000), provides examples of this phenomenon with his observations of European hoverflies that resemble bees and wasps. Several hypotheses exist to explain the existence and persistence of imprecise mimics, as outlined by Edmunds (2000). One such hypothesis, originally proposed by Duncan and Sheppard (1965), suggests that imprecise mimics may persist if their model is considerably defended (e.g., extremely noxious or dangerous). Another hypothesis proposed by Brower (1960) suggests that an ecosystem harboring a diversity of defended aposematic species (and phenotypes) may allow for mimics that do not perfectly resemble any one of the defended species. In such cases, predators may be more inclined to avoid imprecise mimics due to the diminished probability of obtaining a palatable meal. Kikuchi et al. (2009) expanded on this concept, coining the term “cone of protection” meant to describe the instance where the degree of imprecision that receives protection from predators may correspond to the population density of the model and the degree to which the model is noxious. Essentially, in the case that there exists a large number of very noxious models in a given area, an artificial “cone” of protection may engulf both precise and imprecise mimics, affording both with protection (Kikuchi et al., 2009). However, the question of whether certain imprecise phenotypes are more effective at predator deterrence than others remain untested.

Our experiment aims to investigate the Batesian mimicry complex associated with coral snake species and their mimics, assessing the degree to which imprecise mimics of coral snakes are protected from predators. In particular we focus on a type of imprecision, “shifted” patterns, found in many coral snake mimics, particularly in South America. In such examples, the bands that encircle some mimic species are misaligned at the center back of the snake, creating a series of broken rings. Two examples of snake species possessing these “shifted” patterns are *Oxyrhopus guibei* and *O. trigeminus* (see Figure 1, photographs *C.* and *E.*). Interestingly, this shifted pattern is absent from coral snakes and their mimics in the southeastern US. In order to assess the selective forces on imprecise mimics with shifted patterns, we utilized clay snake replicas as have been previously utilized by Pfennig et al. (2006; 2001) and Brodie et al. (1993; 1995). The work of Brodie (1995) indicated that a variant possessing a bi-color banded pattern did not suffer a significantly different frequency of attack than a variant possessing a tri-color banded pattern, while both of these variants were attacked at a frequency statistically lower than a third, cryptic (brown) variant (Brodie et al. 1995). Therefore it might be the case that similar selective forces act on both shifted and non-shifted variants.

MATERIALS AND METHODS

Beginning in the spring of 2019, myself and other participants within the lab of Dr. Brice Noonan began the process of constructing clay replicas of coral snakes. The group constructed three such variants of coral snake replicas: two of which were imprecise, and the third, precise (Figure 2). The imprecise mimic variants possessed a shifted banding pattern, located either directly posterior to the head (front-shifted), or directly anterior to the tail (rear-shifted). The precise mimic variants had no shifted bands and were an accurate mimic of *Micrurus fulvius*. Non-toxic, plasticine modeling clay of the colors: red, yellow, and black, manufactured by Van Aken, was used to construct these replicas. Despite the differing appearances among the three variants, each contained roughly the same proportion of red, yellow, and black plasticine. Each replica measured roughly 28 cm in length.

Replicas (Figure 2) were constructed using pre-assembled cylindrical segments fitted to a length of wire. Each of these segments contained differing proportions of red, yellow, and black plasticine, to reflect the coloration of *Micrurus fulvius* at its tail, its mid-section, and posterior to its head. The segments were attached at their ends in order to form each replica. The head pieces used for all of the replicas were small, oblong portions of black clay, fitted to the end of the wires. The lengths of wire that were used served to improve the structural integrity of each replica while providing each with the ability to be bent into a fixed shape without incurring damage. Replicas were bent in “S” shapes to reflect how they might appear in the wild at any given time.

In order to construct the imprecise "shifted" variants, segments were sliced lengthwise using a razor blade, and reassembled with a misalignment of left/right colored bands. Full-length replicas were then assembled in such a way as to incorporate the shift at either the front (posterior to the head) or rear (at the tail end of the model) in each completed replica, as outlined above. All-in-all, 840 replicas (280 of each variant) were constructed during the time period of spring, 2019 to fall, 2020.

Figure 2: The Three Variants of Plasticine Replicas Utilized in the Study. *A.* Precise mimic variant. *B.* Front-shifted imprecise mimic variant. *C.* Rear-shifted imprecise mimic variant. Each photo was taken during the deployment phase of the data collection. The replicas were placed in the blocks of their respective transects as shown above. Photographs by Matthew R. Hendricks.

Clay models were placed along ten transects, each approximately 2025 meters, in the Apalachicola National Forest on 31 October and 1 November 2020. Three replicas, one of each pattern, were placed at 28 different sites along each transect, making 280 sites total. Within each transect, sites were spaced at 75-meter intervals and transects were mapped using GPS. A measuring wheel was used to ensure accurate distance measurements between sites within a transect. Within each site, replicas (one of each variant) were spaced roughly 2-3 meters apart in the shape of a triangle. Each site with a triangular set of three replicas will be referred to as a “block” going forward. Blocks were placed a standardized distance of 17 meters from the road to ensure consistency and facilitate the collection process. Flagging tape was tied around nearby brush to each block and to the opposite side of the road to serve as a marker. Each transect differed slightly in terms of vegetation, ground water, foliage, and soil. However, all represented viable habitat for coral snakes and their predators. There were some instances in which standing water or other obstructions forced additional spacing between sites. Once placed at their respective positions on each transect, the replicas were left in place for a period 6 weeks (November 1 – December 15). During this period, they were exposed to all natural weather conditions of the area. A map of the Apalachicola National Forest depicting the location of each of the ten transects is shown in Figure 3. (Figure 3).

Replicas were collected December 15 & 16, 2020. Collection consisted of traveling to the locations of each block in a successive manner. Transect by transect, we traveled to each of the sites containing replicas, 280 in total. The collection process was expedited due to the flagging tape which had been previously laid down to indicate the location of the blocks. At each of these locations, the models were collected by hand and labeled according to which block they represented and from which transect. Once marked, each of the models was placed in an assigned storage bin to ensure safe transport to the lab where they were to be examined for evidence of attack. During our experiment each replica was used only once.

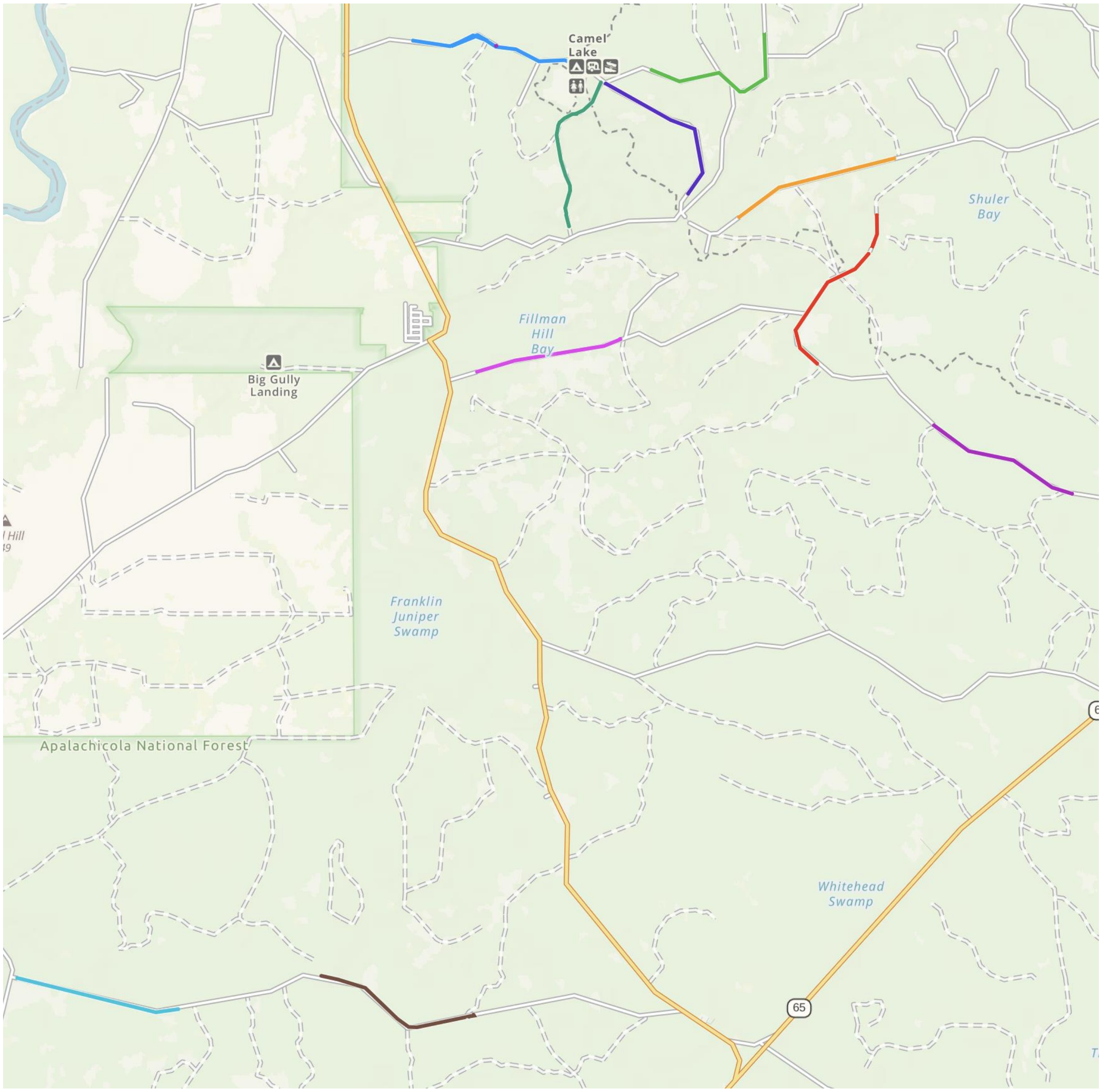

Figure 3: Map of the Apalachicola National Forest Containing Transect Locations. Each colored line segment represents a transect.

Prior to the examination of the replicas for evidence of attacks, they were removed from storage containers and organized according to their transect. For the review of models and recording of attack marks we established a system in which each of the numbers from 0-5 corresponded to a distinct type of observation. This system accounted for all potential attacks left by predators, but also factored in those replicas that could not be found or were disturbed by man (e.g., foot print) or nature (e.g., fallen branch). Replicas that exhibited no signs of attack were assigned “0,” those that were not recovered were assigned “1,” replicas that exhibited signs of attack from an avian species or a species of mammal were assigned “2” and “3,” respectively, replicas that exhibited markings of indistinguishable origin were assigned “4,” and replicas that contained damages that were unnatural (i.e., those resulting from human interference) were assigned “5.” Each of the 840 replicas which were laid out received one of these six designations.

In order to assign a designation to each replica, every model was thoroughly inspected within the lab. In the event of the observation of marks in the clay indicative of an attack being observed, photographs were taken of the marks on the replica and the attack was classified using the numbering scheme described above. Photographs were also taken to document other observations such as damage not caused naturally, as was the case with human interference. For example, several of the recovered replicas had been stepped on, evidenced by the presence of shoe imprints. All replicas which had shown signs of an encounter with a mammal or avian species were designated as such. Brodie et al. (1993) demonstrated that “U” or “V” shape imprints were indicative of marks left by avian species. As such, markings of these shapes were considered to be left by avian species in our analysis as well. Attacks left by larger mammals were judged by the presence of distinct bite and scratch marks. Those left by small mammals were judged by the presence of smaller bite or scratch marks. In some instances, entire segments of the replicas had been gnawed off, leaving little clay attached to the wires. In others, only the wires themselves were found. One final clarification regarding the analysis that holds importance deals with the designation of “4,” which applies to those replicas that bore markings of unknown origin. In the event that the origin of a given replica’s markings could not be determined with a high level of confidence, said replica received this designation. That is, if there was sufficient doubt as to whether a marking was left by a mammalian or avian species, the replica was designated as such. Examples of each designation are shown in Figure 4 (see Figure 4).

We used a generalized, linear mixed-effects model using the package LME4 (Bates, D. 2015) in the software RStudio (RStudio Team, 2020). We modeled the frequency of attack on each phenotype considering the random effects of our nested design (blocks and transects) and compared this model to a null model using an analysis of variance. Since we coded the attack frequencies as either the presence or absence of attack marks, our model incorporated a binomial distribution. To generate the graphs, we used the package ggplot2 in RStudio (Wickham 2016). To better visualize the results of our experiment, a mosaic plot was constructed, which compared the number of attacks to the lack thereof, according to each phenotype (Figure 7).

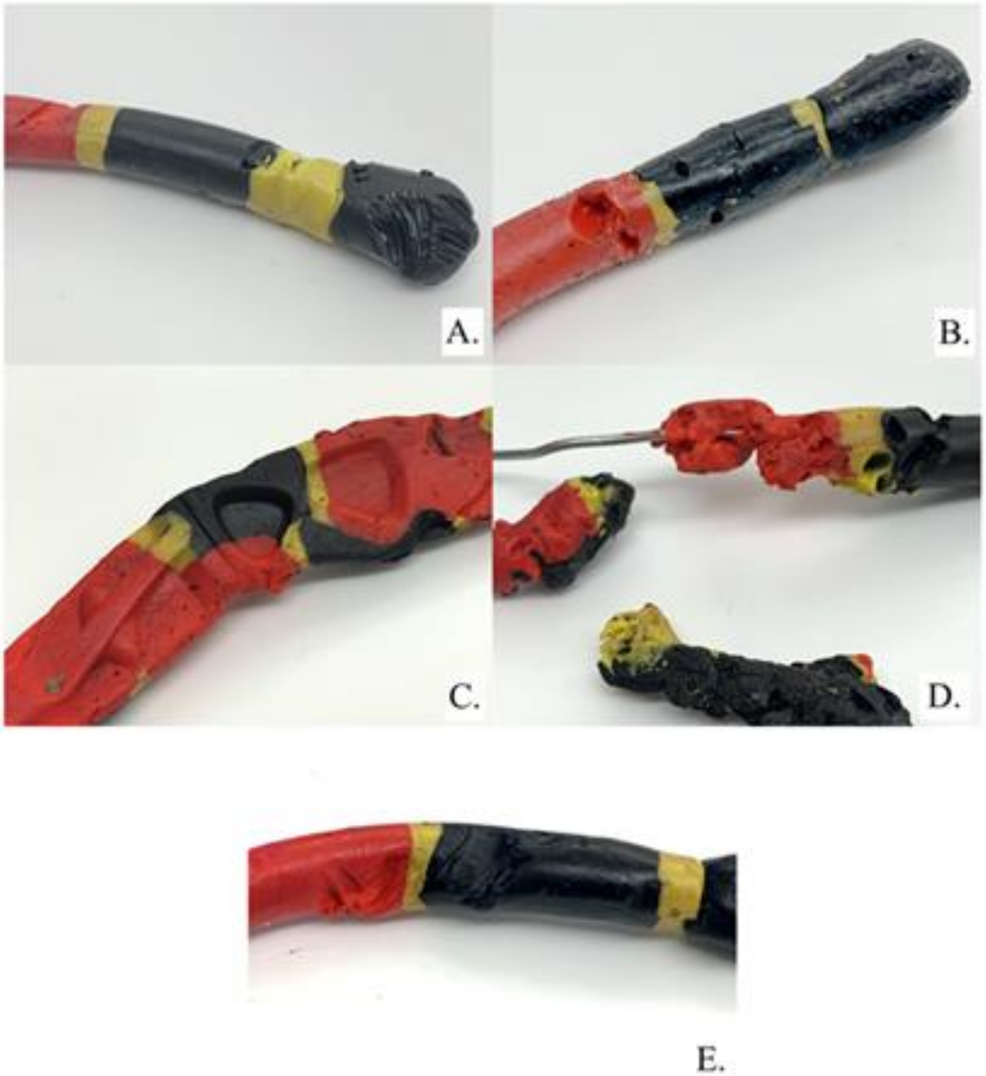

Figure 4: A Visualization of Collected Replicas and their Respective Designations. *A.* Replica attacked by a small mammalian species (designation 3). *B.* Replica attacked by an avian species (designation 2). *C.* Replica bearing a human boot imprint (designation 5). *D.* Replica attacked by a larger mammalian species (designation 3). *E.* Replica bearing markings of unknown origin (designation 4). All replicas pictured were utilized in the field experiment and were photographed during the process of data collection and analysis. Photographs by Matthew R. Hendricks.

RESULTS

Of the three phenotypes, the rear-shifted variant experienced the highest attack frequency, at 15.7% of replicas attacked. Next, was the front-shifted variant, at 13.9% of replicas attacked. Lastly, the precise variant, at 11.8% replicas attacked (Figure 5). In terms of each transect, transect 8 had the highest attack frequency, at 28.6%. The next closest transect was transect 5, at 20.2%, followed by transects 2 and 7, which were each 15.5%. Transect 9 had the smallest attack frequency, at just 2.4% (Figure 6).

There were no differences between our data and a null model in that the attack frequencies on different phenotype variants did not differ significantly from each other (Figure 5) (Chisq^2 = 2.15 $p > 0.34$). The mosaic plot denotes the presence and absence of attacks experienced by each of the phenotypes as rectangles of varying area. Each phenotype is associated with two of these rectangles, one indicating the presence of attacks, the other indicating the absence of them (Figure 7). The results of this plot are consistent with those of the previous models, as evident by the generated rectangles quantifying attacks and the lack thereof on each phenotype being near the same area.

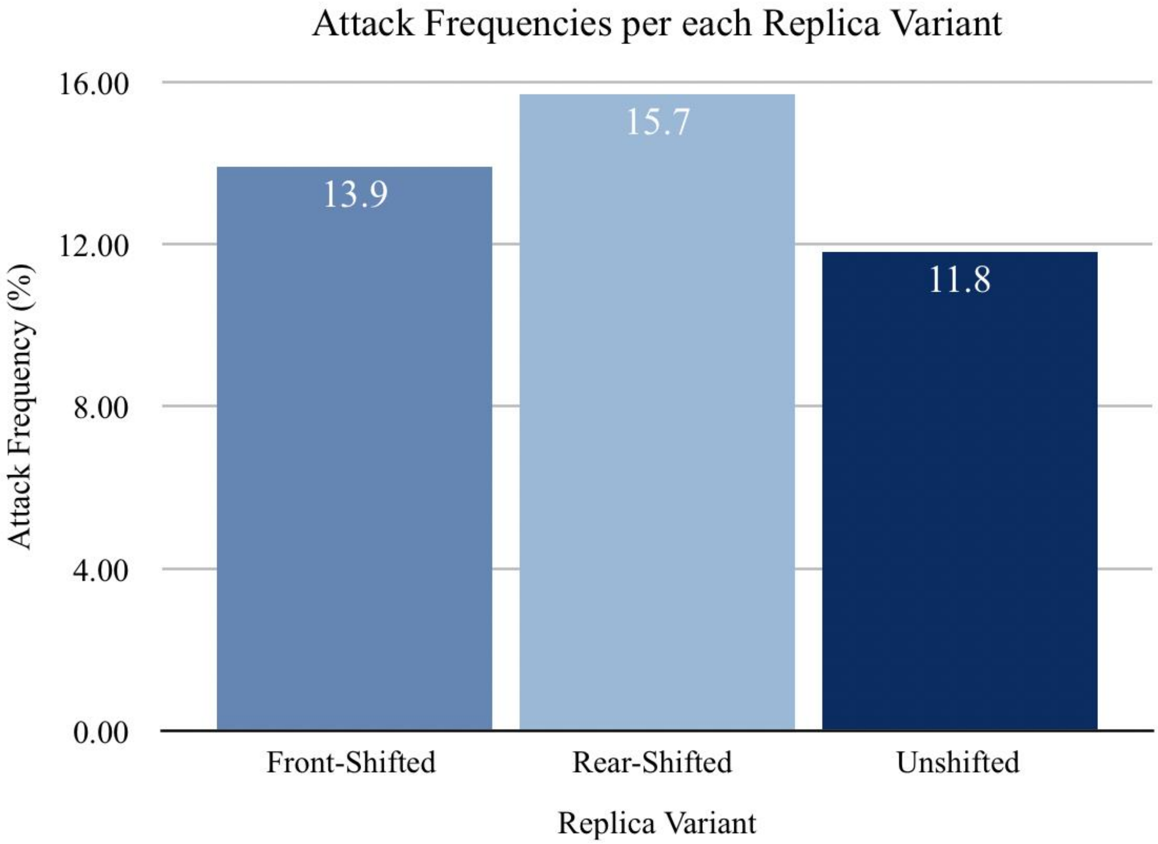

Figure 5: Attack Frequencies per each Replica Variant. The three columns on the x-axis represent each of the three replica variants. The height of each column on the y-axis quantifies the attack frequencies of each replica variant. Each attack frequency is expressed as the percentage of replicas of each variant which bore markings characteristic of predation.

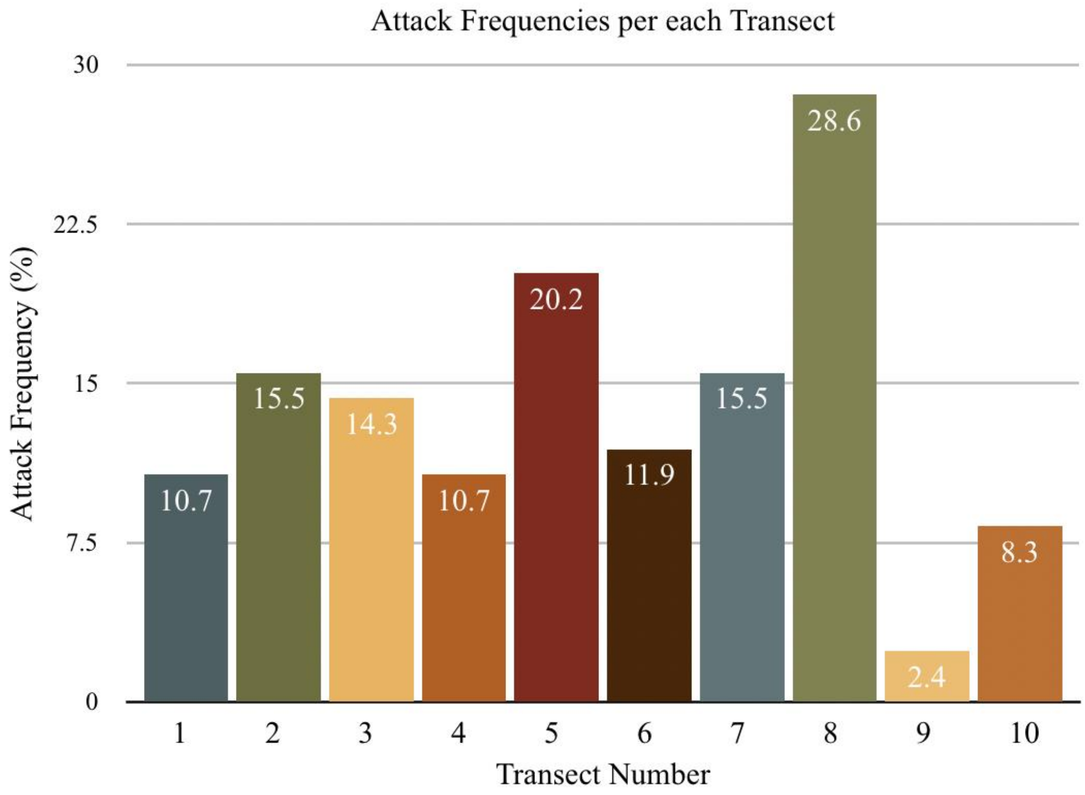

Figure 6: Attack Frequencies per each Transect. Each column on the x-axis represents one of the 10 transects. These columns are arranged in ascending numerical order in terms of each transect. The height of each column on the y-axis quantifies the attack frequencies at each of the transects. Attack frequencies are expressed as percentages of the number of replicas at each transect deemed to have been attacked by a predator.

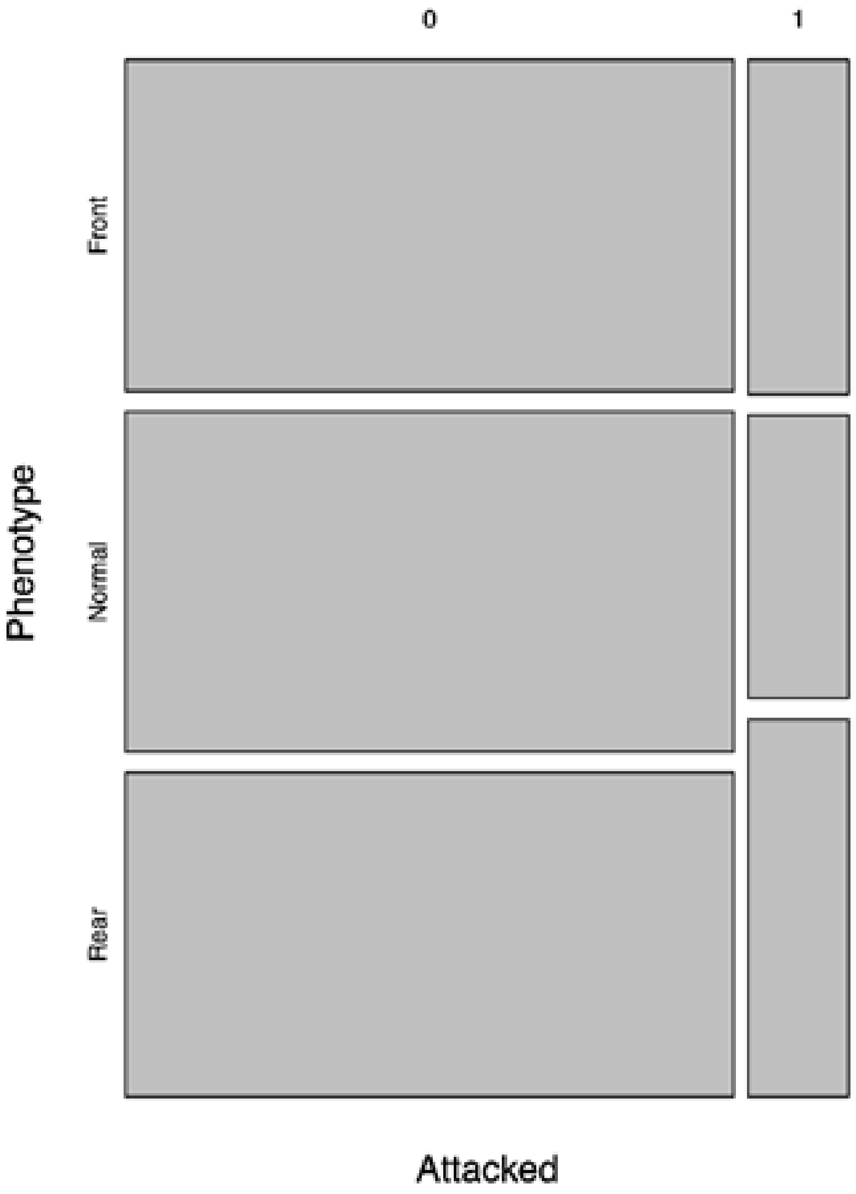

Figure 7: Mosaic Plot Offering a Visual Comparison of the Attacks Recorded for each Replica Variant. The size of each rectangle serves to quantify the number of replicas which fit each condition (attacked; not attacked). The three rectangles beneath the 0 column quantify the number of replicas per phenotype which were not attacked while the rectangles beneath the 1 column quantify the number of replicas per phenotype which were attacked.

DISCUSSION

Overall, our results suggest that there are no selective advantages (or disadvantages, for that matter) experienced by mimics with imprecise phenotypes, when compared to those that are precise. This is made evident by the analysis of our results, which indicates that the differences in the attack frequencies on each of the imprecise variants to those of the precise variant were not statistically significant.

The work of multiple researchers can be cited to explain our findings. The work of Duncan and Sheppard (1965) involving the effects of high model toxicity on the persistence of imprecise mimics and that of Lindström et al. (1997) regarding high model abundance, for example, offer potential explanations for the persistence of imperfect mimicry. Duncan and Sheppard (1965) document that in the case an encountered prey animal is highly noxious, predators are more likely to overlook differences in mimetic phenotypes, which can provide for the evolution and persistence of imprecise phenotypes (Duncan et al. 1965). In their investigation it was also noted that, in the case an encountered prey animal poses little threat, predators are not inclined to overlook the differences in mimetic phenotypes. Lindström et al. in Lindström et al. (1997), note that predators may also overlook mimetic phenotypes in the case that the model species is highly abundant. In their experiment, mimic mortality rates were indeed lower when the number of models was sufficiently high. This case may be made with coral snakes, as they are both highly noxious and widely distributed throughout the Southeastern US (Ackali et al. 2018).

In a 2009 study, Kikuchi et al., touching on the work of Duncan and Sheppard (1965) and Lindström (1997), examine the proposed evolution of Batesian mimicry from cryptic phenotypes and whether the selective disadvantages of intermediate phenotypes increase directly with model abundance (Kikuchi et al. 2009). Kikuchi et al. (2009) suggest that it is likely that the same circumstances contributing to the evolution of imperfect mimicry may also allow for fitness advantages for intermediate phenotypes. Within their investigation, Kikuchi et al. (2009) mention the concept of a “cone of protection” This concept suggests that when a model poses substantial threat to potential predators, intermediate or imprecise phenotypes of the highly noxious model’s mimics may remain protected. Essentially, the benefit of attacking one of these “imprecise” species is outweighed by the risk associated with the potential that the organism may, in fact, be noxious. Therefore, when a predator is experienced with a highly noxious model such as *Micrurus fulvius*, it may be inclined to avoid an array of mimetic phenotypes, which may encompass the shifted patterns utilized in our experiment.

In light of our findings, another important distinction can be made regarding our experimental design. Specifically, it is unlikely that predators noticed all three phenotypic variants simultaneously, as the replicas were placed sufficiently far apart from each other (2-3 meters). Thus, it is unlikely that predators were consciously choosing to attack one phenotype over the others for the vast majority of our blocks. In a 1988 publication, Hetz and Slobodchikoff incorporated a system of “spontaneous choice” within their experiment involving the predation pressure on a Batesian mimicry complex in which alternative prey is included (Hetz et al. 1988). For example, predators were exposed to not only mimics and their models, but also an alternative prey species. Their results indicate that the alternative prey species was attacked at a higher rate than both the mimic and model. The mimics in their experiment were also attacked more than the models, however (Hetz et al. 1988). When predators have the choice between noxious models (and their mimics) and a palatable alternative, they more quickly learn to avoid the mimicry complex in favor of the alternative prey (Slobodchikoff 1987). In light of their findings, it would be reasonable to expect that, had our design provided predators with simultaneous choice, the incorporation of a phenotypic variant that serves to represent an alternative prey animal might have yielded different results. Thus, to gain further insight regarding the selective forces acting on both precise and imprecise phenotypes, it might have been beneficial to include a replica variant representative of "alternative prey" within our experimental design, in addition to a system which incorporated simultaneous choice.

Another probable explanation for the similarly low frequencies of attack on each of our replica variants is the probability of innate avoidance of banded patterns such as those found on coral snakes and their mimics among predators. Brodie et al. (1995) in an experiment based in Costa Rica that utilized a similar experimental design to our own, demonstrated that avian predators had indeed generalized avoidance of ringed patterns. They suggested that this generalized avoidance had materialized either through the result of learned experience or through an innate avoidance resulting from evolution (Brodie et al. 1995). Their experiment involved the use of two variants of banded replicas (one that was bi-colored and one that was tri-colored) and one brown replica. Brodie et al. (1995) note that it was unlikely that avian predators in the geographical area of their study had been exposed to the bi-colored variant, a situation similar to the novel shifted models we tested in Florida. The differences in attack frequencies between the brown replica and the two, colored replicas was indeed statistically significant. The fact that predators avoided the bi-colored phenotype despite likely never having experienced it suggests that these predators possess an innate avoidance of banded patterns, even when novel. Just like the bi-colored phenotype used in the experiment of Brodie et al. (1995), two of the replica variants used in our investigation (those with front and rear-shifted patterns) also had likely never been experienced by predators. Therefore, because there were no statistically significant differences in the attack frequencies for each of the replica variants used in our study, it may be concluded that predators in the southeastern US may also possess an innate, generalized avoidance of banded patterns.

Dittrich et al., in a 1993 publication, present very interesting findings involving the potential differences in the processes of perception of humans and animals. Their study assesses the degree to which pigeons perceive hoverflies of varying phenotypes as being good and poor mimics of a wasp, *Vespula vulgaris*. In their experiment, pigeons were chosen to represent avian predators. Dittrich et al. note in their findings that human perception in terms of what is a “good” and “poor” mimic differs from that of the pigeons used in their experiment. Specifically, the species *Syrphus ribesii* and *Episyrphus balteus* (see Dittrich et al. 1993, Fig. 1f and 1d, respectively) are judged by humans to be relatively poor mimics of wasps. In contrast, the same species were judged by the pigeons to be the best of the mimics sampled. Therefore, these results suggest that what is a good mimic in the eyes of a human may be a poor mimic in the eyes of a particular predator, and vice versa. Furthermore, the characteristics of a species which indicate that it is good or poor mimic to another species may be entirely different for humans than for other species. Thus, in light of these findings, it may be suggested that there is a likelihood that the imprecise phenotypes we used in our experiment did not appear as such to the predators which encountered them. Rather, all three phenotypes used may have been judged as high-fidelity mimics, due to perceptive differences in the predators. This represents a possible explanation of our findings, as there were not any selective advantages nor disadvantages experienced by any of the three phenotypes employed in our experiment.

An additional explanation of notable importance involves the geographical distribution of coral snake species and their mimics, as studied by Ackali et al. (2017). The results of their experiment indicate that mimetic precision varies according to the geographic distribution of model species (Ackali et al. 2017). It was noted that the precision of coal snake mimics in sympatry with their models was highly variable. Specifically, they examined four Batesian mimics of coral snakes whose distribution occurs where models are not only abundant and rare, but also completely absent. One of these mimic and model pairs was *Micrurus fulvius* (the model) and *Lampropeltis elapsoides* (the mimic). They noted that the precision of *L. elapsoides* to its model was highest at the sympatry-allopatry boundary and it declined in allopatry. The Apalachicola National Forest, where our investigation was conducted, is located in an area in which mimetic precision is intermediate (see Ackali et al. 2017 Figure 1a). Therefore, due to the persistence of mimics that do not fully resemble their models, it logically follows that they receive some protection from predators. Our findings seem to reflect this, as none of our variants fared better than the others, despite the imperfect resemblance of two of the variants.

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