The Evolution of Mimicry

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Introduction

Cryptic species have evolved camouflage, which enhances survival by decreasing their visibility and thus protecting them from would-be predators. Conversely, aposematic species have evolved vibrant colors which enhance visibility. These warning signals work by helping unpalatable, toxic, evasive, or stinging prey stand out from more favorable prey. Thus, predators learn to generalize the appearance of prey which taste bad or can inflict pain (Balogh 2005).

Yet, all species with aposematic coloration do not have other unfavorable features. These species, known as Batesian mimics, have evolved to look like model species which are unprofitable to predators (Mappes 1997). Thus, Batesian mimicry enhances survival of otherwise unprotected species, while increasing the attack rate of the model species and deceiving the predator (Ritland 1991). As such, Batesian mimicry is part of an evolutionary exploitative relationship, in which the mimic derives benefit at the prey and predators expense.

Conversely, Müllerian mimicry, in which two (or more) unfavorable prey species share similar physical characteristics, actually benefits all of the directly involved species. Since the co-mimics are unfavorable and similar in appearance, Müllerian mimics are less likely to be consumed by predators. The predators benefit because they do not have to suffer the consequences of consuming the unfavorable prey. Thus, Müllerian mimicry is a complex evolutionary mutualism which enhances survival of the involved prey and predators alike (Gavrilets 1997).

There are many questions regarding the evolutionary pathway of mimicry which have not yet been elucidated. Two theories have been proposed to explain the pathway of Müllerian mimicry. The first theory, developed by Nicholson in 1927, is known as the two-step hypothesis. In this theory, evolution occurs first due to a large mutational change which causes a mimic to appear more similar to a model. After this large mutational change, the second step is a gradual change (Balogh 2005). Conversely, Fisher (1927) proposed the gradual hypothesis which is driven by predator generalization. This theory states that mimicry occurs from many small mutations each of which slightly increase the similarity between the mimic and the model. While eighty years have passed since these two theories were developed, the evolutionary path for Müllerian mimicry has still not been elucidated.

Many other questions regarding the evolution of mimicry also still exist. For instance, the role of selective forces such as varying mortality rates among mimics and models in Batesian mimicry, population dynamics and associated ecological interactions, and the driving force for aposematic coloration have still not been elucidated. Furthermore, the role of imperfect mimicry, if any, in the evolution of mimicry has not been

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deduced. This review is a comprehensive analysis of primary literature focusing on addressing these evolutionary issues, while also evaluating the two-step hypothesis and the gradual hypothesis of Müllerian mimicry.

Mathematical Modeling of Mimicry

Mathematical and computerized modeling systems are commonly used to mimic the evolution of mimicry. This methodology is advantageous because it enables scientists to study avoidance learning. Modeling studies require many assumptions, because it is hard to create a system exactly like the wild. For mimicry, studying the interactions and development of avoidance learning is extremely difficult in the wild. This is the biggest single advantage for mathematical models.

Gradual Evolution or the Two Step Hypothesis of Evolution of Mimicry

Balogh and Leimar (2005) created a computerized mathematical model to investigate gradual evolution as defined by Fisher (1927) through utilizing a Müllerian mimicry predator spectrum. In the model, predators generalize their experience with unpalatable prey causing them to avoid prey similar in appearance to the unpalatable prey (Balogh 2005). The model predicted that gradual evolution, as defined by Fisher (1927) occurs in Müllerian mimicry systems by showing that evolution toward mimicry occurred through predominantly small peak shift mutations. Having a variety of predators with different generalizing specificities increased the gradual shift (Balogh 2005). Thus, ecosystems with multiple predators are more likely to demonstrate gradual evolution of Müllerian mimicry, and coevolutionary changes frequently play a role in Müllerian mimicry evolution.

Through replicating Balogh and Leimar's (2005) model and modifying it slightly, Franks and Sherratt (2007) studied gradual evolution of multiple components. Through this, their model suggested that gradual evolution is only possible when only a single component or characteristic is being mimicked or the predators generalize widely over all components. In other words, multicomponent Müllerian mimicry tends to evolve via the two step hypothesis of evolution, which states that mimetic evolution occurs initially as a result of a large mutational change in prey which closely resembles a model species, and over time, smaller mutations refine the phenotypic similarity to the model species (Turner 2000). Still, under certain ecological circumstances, gradual evolution is the rule, and in fact, the two theories are not necessarily mutually exclusive.

Ecosystem Dynamics as a Selective Force for the Evolution of Mimicry

To evaluate the selective forces involved in the selection of Müllerian mimicry, Beatty (2004) simulated predator/pray relationships via a computer program which examined avoidance learning in human predators by allowing them to search a virtual environment for prey. The study consisted of five separate experiments. The first experiment utilized a simple system in which predators were exposed to an equal amount of profitable and unprofitable prey. The profitable prey was all green, while the unprofitable prey

was split into nine different frequencies of green and blue prey. In all, the experiment demonstrated that rare forms of unprofitable prey are eaten more frequently than common forms of unprofitable prey (Beatty 2004). Because of this, there is a selective force for uncommon unprofitable prey to mimic common unprofitable prey. The second experiment also utilized a simple system in which profitable prey was yellow, non-focal unprofitable prey was blue with a stripe, and the focal prey varied per trial (solid pink, black dot with pink background, or pink with black stripe). Among the three focal prey, each was selected equally demonstrating that Müllerian mimicry is not favored in simple communities (Beatty 2004). Thus, in communities in which predators have limited prey options, there is little to no driving force toward Müllerian mimicry.

Beatty (2004) also analyzed Müllerian mimicry within communities including predators with multiple prey options. In experiment three, six different profitable prey shared a common characteristic in which they were all solid colored. Likewise, the six non-focal unprofitable prey shared a black stripe. Similarly, in experiment four, half the profitable prey had stripes as did half the unprofitable prey did as well. In both of these experiments, three focal unprofitable prey of the same color but different physical characteristics (solid colored, striped, and circular dot) were used to determine the relationship between perfect mimicry and imperfect mimicry in multispecies communities. The model suggested that when unprofitable prey share physical characteristics, mimics that also share these characteristics are less likely to be eaten. However, when no physical characteristic is associated with profitability, then there is no difference in preference amongst the focal unprofitable prey. Furthermore, Beatty (2004) found that imperfect mimicry which increases the similarity of one unprofitable prey to another more common unprofitable prey enhances the survival rate of the mutant. These results suggest predators generalize avoidance learning. Instead of determining if each prey is unprofitable, they notice physical characteristics which are common among unprofitable prey. As such, there is a selection force in communities containing multiple species, which tends to enhance Müllerian mimicry amongst unprofitable prey.

Using a different mathematical model, Holen and Johnstone (2004) demonstrated differing results regarding population dynamics for Batesian mimicry. Primarily, the model suggested that if Batesian mimics are too common in an ecosystem, or the Batesian mimics mimic poorly defended organisms, then stabilizing selection can cause inaccurate mimicry or mimetic polymorphism. This is enhanced in circumstances in which the Batesian mimics are exposed to exposure to high numbers of predators or are bad at evading attacks (Holen 2004). Gavrilets and Hastings (1998) created a model which suggested similar results in a simple two-species system. Taken together, these results suggest that Batesian mimicry requires tight ecological interactions between the mimic and the operator (that is the organism being mimicked).

Evolution of Evasive Mimicry
Evasive mimicry was first noted in 1971 when Lindroth discovered that certain mimics produce no unpalatable chemicals (Ruxton 2004). Further research has demonstrated that some of these mimics do not share an identifiable common descent (Ruxton 2004). To

investigate whether Müllerian and Batesian mimicry based on difficulty to capture is theoretically possible; Ruxton and associates (2004) created two homologous mathematical models. The model demonstrated that Batesian mimicry is theoretically possible when predators have another food source, and pursuing evasive prey is energetically unfavorable. Conversely, Müllerian mimicry is most likely to occur in situations in which evasion is costly to the prey, predators learn avoidance slowly, and the abundance of evasive prey species is not the same. Thus, based on these mathematical models, the evolution of evasive mimicry should be common under the right conditions.

Signal Accuracy and Initiation of Mimic Evolution
The widespread occurrence of aposematic coloration has been linked to predator learning (Lindström 2001). Sherratt and Beatty (2001) investigated this claim by using a computerized model utilizing human predators and studying the responses of human predators to defended and undefended computer-generated prey species. The findings suggested that the evolution of warning signals has less to do with aposematic coloration avoidance. In fact, the model suggested that cryptic species which are well defended are also avoided by predators. As such, they found aposematic coloration evolves primarily because it sets species apart from undefended prey (Sherratt 2001). This modified hypothesis adjusts for the fact that predator learning also applies to cryptic species which have a different physical appearance than unprotected prey.

Johnstone (2002) created a mathematical model to investigate the evolution of accurate and inaccurate mimicry. Through this model, he found that accurate mimicry is favored when the models are either extremely aversive (toxic, unpalatable) to the predator, or the model is much more common than the mimic. Likewise, inaccurate mimicry is more likely when the models are relatively non-aversive, or the model is less abundant than the mimic. Furthermore, inaccurate mimicry is favored among organisms which have small ranges, limited dispersal, and high levels of inbreeding (Johnstone 2002). These findings represent theoretical guidelines for the evolution of accurate and inaccurate mimicry.

Biological Models of Mimicry

The evolution of mimicry is hard to study in the wild. To combat this, many scientists study signal generalization and mimicry through exposing captive organisms to unpalatable food with certain physical characteristics (such as color or design). Through using these techniques, scientists get determine how long it takes for predators to use stimulus generalization in avoiding food with certain appearances. Ultimately, this technique can be used to address several key issues involved in understanding the evolution of mimicry.

Evolution of Evasive Mimicry
As discussed previously, the evolution of evasive mimicry under certain circumstances has been demonstrated theoretically using two mathematical models. Evidence for Batesian mimicry has also been shown experimentally. In one such experiment, Gibson (1974) gave star finches seeds dyed red, blue, and green. The green seeds were available for the birds to eat, but once the birds stepped on the platform to get the red or blue seeds, the platform tilted, disabling the birds from getting the seeds. Through this technique,

the birds demonstrated aversion to the red seeds for two weeks after the experiment. The birds also demonstrated initial aversion to the blue seeds, but due to possible cryptic coloration between the green and the blue seeds, the aversion period did not last as long. In a similar experiment using European robins, Gibson (1980) found similar results using dyed mealworms. These experiments demonstrated that evasive mimicry is indeed plausible; however, the study would have been improved if another seed featuring cryptic coloration with the red seeds was used.

Hancox and Allen (1991) found similar results in another experiment using uncooked dough dyed red and yellow and various garden birds. In this experiment, a slight initial preference for the yellow uncooked dough was noticed in day one. For the next three weeks, when birds went for the yellow dough, a withdrawal mechanism took the yellow dough away. After 21 days, the red dough was favored 28 out of 43 times. Then, the red dough was made evasive for two weeks, and after that time period, the yellow dough was favored 28 out of 38 times (1991). This experiment also lacked appropriate cryptic coloration techniques for a proper investigation of Batesian mimicry, and likewise, removing the dough rapidly could have initiated a startling effect. Assuming the startling effect was not significant; this experiment also demonstrates that evasive learning among prey can influence predator choice.

Signal Accuracy, Aggregation, and Initiation of Mimic Evolution
Mappes and Alatalo (1997) sought to investigate the accuracy of the initial mimetic signal required for evolution of Batesian mimicry. They addressed this question by feeding great tits (*Parus major)* palatable and unpalatable food with distinct appearances. Through this, they conditioned the birds to prefer foods of a certain appearance. They then exposed birds to food with intermediate designs to study the strength of the evolutionary stimulus. The results showed that while there is a strong selection for perfect mimicry, Batesian mimicry can evolve through imperfect but drastic mutations which enhance similarity toward an unpalatable model species (Mappes 1997). In other words, the evolution of perfect Batesian mimicry is not instantaneous, and in fact, it begins with one imperfect initial change. In contrast, Huheey (1976) suggested that Batesian mimicry actually evolves when speciation among Müllerian mimics causes evolution of a novel species without aposematic features but no unfavorable traits. These two alternative explanations are not necessarily mutually exclusive.

In a similar study conducted by Alatalo and Mappes (1996), the initiation of Müllerian mimicry was also found to occur initially through imperfect mutations, and gradual selective forces lead to perfect mimicry. Furthermore, this study suggested that Müllerian mimicry evolves partially through prey aggregation. That is unpalatable prey in view of potential predators are more likely to be ignored if they have similar physical characteristics. This view correlates with Fisher's (1930) idea of kin grouping, which states that related organisms will aggregate, but it does not necessarily mean aggregation occurs. Guilford (1991) supported kin grouping, but also suggested that other stochastic methods of aggregation play a larger role in the evolution of Müllerian mimicry. Together, aggregation seems to play a role in the initiation of the evolution of Müllerian mimicry, which stems from the idea that predators generalize their feeding patterns, and by looking similar, unpalatable or undesirable prey enhance their survival.

To analyze the driving force behind the evolution of aposematism, Lindström and colleagues (2001) fed wild great tits (*Parus major*) various frequencies of novel conspicuous aposematic which was either dispersed or solitary. The results suggested that avoidance learning was the selective force behind the evolution of aposematism, and this avoidance learning occurred after only six days. Furthermore, aggregated aposematic prey was consumed less frequently than solitary prey (Lindström 2001). Combined, this experiment suggests that aposematic evolution occurs primarily due to predator learning and is enhanced by aggregation.

In a similarly designed experimental novel environment, Lindström, Alatalo, and Mappes (1997) investigated imperfect Batesian mimicry through great tits. They found that imperfect mimics were most likely to survive when greatly outnumbered by the model species. Moreover, if mortality of the mimic is high, selective forces enhance the similarity between the mimic and the model. Conversely, if mortality of the model is high, selective forces drive the model to become less palatable (1997). Implications of this study suggest a highly regulated system of evolution and regulation of Batesian mimicry exists with naturally fluctuating driving forces.

Biological Systems

A few of the studies focused on biological systems and interactions between real predators and prey, as well as the relationships between model species and their mimics. These studies looked at toxicity levels, geographic range, and phenotypic similarity between related mimic species

Initiation of Mimic Evolution
As mentioned previously, Johnstone (2002) predicted that Batesian mimics will favor the most abundant and/or noxious model. Also, Lindström (1997) demonstrated this in a biological model. Darst and Cummings (2006) decided to analyze this prediction by studying two Ecuadorian poison frogs (*Epipedobates bilinguis* and *Epipedobates parvulus*) and a geographically dimorphic, phylogenetically distant, nonpoisonous relative (*Allobates zaparo)*. They found that *A. zaparo*, which mimics both *Epipedobates* species in areas in which the species are geographically separate, mimics only *E. bilinguis* in areas in which the geographic distribution of the two species overlaps. Additionally, *E. bilinguis* is less common than *E. parvulus* in these areas, and also less toxic. Darst and Cummings (2006) explained this by demonstrating that the generalized avoidance curve for predators that eat *E. parvulus* covers *E. bilinguis*, while the reverse is not true. In other words, *E. parvulus* causes generalized avoidance learning, while *E. bilinguis* causes only specialized avoidance learning (Darst 2006). Thus, by mimicking the rarer, less poisonous *E. bilinguis*, *A. zaparo* obtains protection from predators which have learned to avoid both *Epipedobates* species.

The relationship between Florida viceroy butterflies and Florida queens has been described as Batesian mimicry in which the viceroys mimic the unpalatable queens for 120 years. Ritland (1991) reinvestigated this relationship by determining the

palatability of each species. Through this, both species were found to be unpalatable, but this unpalatability varied among local populations. As such, Ritland (1991) theorized that the relationship of the viceroys with the queens might be Müllerian comimics in some areas, Batesian mimics in others, and even Batesian models in others. If Ritland's hypothesis is true, then the evolution of mimicry and aposematism might be much more intrinsically tied together in Müllerian mimicry than originally thought. In fact, Batesian mimicry might evolve from Müllerian mimicry, but Müllerian mimicry might also evolve from Batesian mimicry. Furthermore, these various evolutions might both occur in various microhabitats.

Discussion

Gradual Evolution or the Two Step Hypothesis of Evolution of Mimicry
Two mathematical models analyzed Fisher's (1927) theory of gradual evolution of mimicry and Nicholson's (Balogh 2005) two-step theory of mimetic evolution. Balogh's (2005) model suggested that in multiple predator systems, the driving force of evolution occurs gradually. While Franks and Sherratt (2007) acknowledged that gradual evolution is possible, their model demonstrated it is only possible when a single component is being evolved. Thus, multi-component mimicry occurs solely through Nicholson's two-step hypothesis. In another mathematical model, Beatty (2004) found that even imperfect mimicry towards an unfavorable model enhances survival. This favors the two-step hypothesis since it demonstrates that one mutation increasing the similarity between a mimic and a model organism increases survival of the mimic even if it is imperfect, and thus, evolving such mutations enhance survival. Two other biological models have shown that imperfect mimicry often occurs first and then gradual evolution leads to more perfect mimetic forms (Alatalo 1996; Mappes 1997). These studies support the two-step hypothesis. Combined, the two-step hypothesis and gradual evolution are not mutually exclusive, and in fact, each method of mimetic evolution is possible given certain parameters. Franks and Sherratt (2007) mentioned this acceptance of both theories under certain circumstances; however, it is likely that there are more factors involved in the mechanism of mimetic evolution.

Ecosytem Dynamics as a Selective Force for the Evolution of Mimicry
Ecosystem dynamics play a crucial role in regulating the evolution of mimicry. In one mathematical model, Beatty (2004) demonstrated that Müllerian mimicry is unlikely in simple ecosystems consisting of only a few prey options, but is much more probable in ecosystems consisting of many prey options. This is largely because predators tend to generalize characteristics of unfavorable prey, so there is a driving force towards unpalatable or otherwise unfavorable species to share common attributes. While Beatty (2004) did not specifically mention this, these circumstances should provide a driving force for Batesian mimicry as well since survival of favorable prey would be enhanced by mimicry as well.

Indeed, several studies have demonstrated that Batesian mimicry is highly dependent on tight ecological interactions. Two mathematical models have suggested that if the population of Batesian mimics is too high, selective forces will tend toward imperfect mimicry or mimetic polymorphism, which would likely decrease survival of the mimics (Gavrilets 1998; Holen 2004). Utilizing a biological model, Lindström, Alatalo, and Mappes (1997) framed their findings in a different light, suggesting that as mimic mortality increases, there is a driving force toward perfect mimicry, and furthermore, as model mortality increases, there is a driving force toward less palatable or other unfavorable characteristics. Thus, ecosystem regulation and population dynamics are crucial in the evolution of Batesian mimicry. By extension, declining populations of co-mimics would likely cause increased expression of unfavorable traits and more perfect Müllerian mimicry as well.

Evolution of Evasive Mimicry
While evolution for mimicry among unpalatable species has been thoroughly study, less research has investigated evasive mimicry. Ruxton (2004) used a mathematical model to determine if evasive mimicry is possible in the wild. The model suggested that evasive Batesian mimicry is driven by the predator. Specifically, it is only possible if avoiding evasive models is energetically favored, and there are alternative food sources. Conversely, evasive Müllerian mimicry is driven by prey and predator related factors. If evasion is costly to prey, the abundance of prey species is not equal, and predators develop learning slowly. This model provides guidelines for the evolution of evasive mimicry which has been induced in several biological models (Gibson 1974; Gibson 1980; Hancox and Allen 1991). Furthermore, it suggests that evasive mimicry is possible under certain circumstances, although these circumstances are relatively uncommon.

Initiation of Mimetic Evolution
A widely accepted hypothesis in mimetic evolution states that this evolution is driven by avoidance learning of aposematism by predators (Lindström 2001). However, this hypothesis has recently been challenged by Sherratt (2001) who developed a mathematical model to investigate this hypothesis. Sherratt found that cryptic colored species which are properly defended also cause avoidance learning in predators. Thus, aposematic coloration is not as important in the evolution of mimicry as standing out from other prey. This finding is fairly logical. If a cryptic unpalatable is placed on a white floor, unable to utilize camouflage, predators will still learn to avoid it as long as it appears distinctly different from other prey (and presumably, it does look different than non-cryptic prey). Thus, predator avoidance of aposematic coloration is likely not the mechanism in which mimetic evolution evolves. Instead, mimetic evolution occurs because unpalatable/unfavorable prey develop a distinct appearance from unprotected prey.

The initiation of mimetic evolution has long been hypothesized to involve aggregation of prey. Initially, this theory came from Fisher who developed the idea of kin grouping, or aggregation of related species (1930). However, several studies have demonstrated that aggregation that enhances development of avoidance learning occurs primarily stochastically (Alatalo 1996; Guilford 1991; Lindström 2001). These studies, each of which utilize biological models, find that mimetic evolution is dependent on the predators seeing mimics and models together, and that through this exposure, avoidance learning is generalized.

Evolutionary Regulation of Mimetic Relationships

One theory regarding the evolution of Batesian mimicry states that Batesian mimicry originates from Müllerian mimicry in which speciation has left some species with similar aposematic coloration, but no unfavorable defense features (1976). Ritland (1991) suggested that in the case of Florida queen and viceroy butterflies, the relationship is Müllerian in some areas and Batesian in others. This suggests that mimetic relationships may fluctuate depending on certain circumstances, and that in fact, these fluctuations may occur within species. As such, it is possible that Batesian mimicry may evolve through Müllerian mimicry, but also Müllerian mimicry may evolve through Batesian mimicry given the right circumstances. While much future research is needed to test this, the implications of this demonstrate that mimetic relationships are highly regulated based on various factors within ecosystems.

Batesian Evolutionary Relationships

One mimetic paradigm is that Batesian mimicry should favor the most abundant and/or most noxious model (Lindström 1997; Johnstone 2006). However, Darst and Cummings (2006) demonstrated in a biological system that through mimicking the less common, less toxic model, Batesian mimics are protected from predators who have consumed both the most toxic and the least toxic model. The reason for this is because the predators whom consume the most toxic model have more generalized aversion learning than do those of the less toxic model. Thus, by mimicking the less toxic model, the mimic is protected by predators that have eaten the less toxic model and the more toxic model. This finding challenges the existing paradigm regarding the driving forces behind the evolution of Batesian mimicry.

Critiques and Suggestions for Further Research

One of the biggest criticisms of the literature is that there are relatively few papers done in biological systems. While mathematical and computer models are useful in ecology, each model is dependent on a number of assumptions. Likewise, biological models also require key assumptions. Most importantly, the novel prey is assumed to cause effects similar to would be wild prey. Studying pure biological system reduces the number of assumptions, and observations in the wild are crucial in confirming or denying the findings of mathematical or biological models. Biological models, likewise, are preferred over mathematical models, as they are experimental in nature. This is not to say mathematical models are not important. Theoretical approaches to biology are integral in enhancing understanding of biological systems, and often, they help drive experimental research. However, conclusions from theoretical models have less significance than research on biological models or systems.

Yet, studying mimicry in the wild is challenging for a number of reasons. First of all, tracking the prey and the predators is difficult to do in a non-invasive manner. Secondly, ecosystems are complex, and there are many confounding factors, such as additional food sources for the predators or seasonal diet changes. Finally, understanding the evolution of mimicry is hard if all the organisms have already evolved. That is to say, in the wild, predators will have already developed avoidance learning, and as such will avoid unpalatable prey (and successful mimics).

Despite these difficulties, a few studies have been able to focus their experiments on biological systems.

To circumvent many of these challenges, future study in mimicry should focus largely on genetics. By understanding the similarity of key loci in mimics and models, the evolutionary framework of mimicry can be further elucidated. These studies will explain the role of convergent and divergent evolution in the development of mimicry through determining the homology of species involved in mimetic relationships. Some studies, such as Joron and colleagues (2006) are already investigating the role of genetics in the evolution of mimicry. In the future, genetics studies will and should become more common in mimicry research.

Conclusion

This review of the literature includes several separate conclusions which help address some of the many complex issues involved in understanding the evolution of mimicry:

1.) Fisher's gradual evolution and Nicholson's two-step hypothesis each play important an important role in mimetic evolution under certain ecological circumstances.

2.) Müllerian mimicry is more probable in multispecies communities.

3.) Batesian mimicry is highly regulated by ecosystem dynamics.

4.) It is likely that Müllerian mimicry is also highly regulated by ecosystem dynamics, and Batesian mimicry is also more probable in multispecies communities.

5.) Evasive mimicry is possible under certain rare conditions.

6.) Stochastic aggregation plays a big role in initiation of mimetic evolution.

7.) Having a different appearance than profitable prey is more important than having aposematic coloration in the initiation of avoidance learning in predators.

8.) It is possible for the type of mimetic relationship to vary within species, which suggests the potential for evolution from Batesian to Müllerian mimicry and vice versa.

9.) In Batesian mimicry, it is advantageous for mimics to mimic the less toxic model in certain circumstances.

Clearly, this review addresses a variety of issues involved in the evolution of mimicry. By and large, more experimentation is needed to verify the conclusions of this review.

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