Allopatric Mimicry

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for
Evolutionary Ecology

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Introduction

Sometimes a harmless or edible species (a mimic) is protected from predation by its resemblance to a species that is dangerous in some way (a model). Such a strategy is known as batesian mimicry. Numerous cases of this phenomenon exist. For example, a harmless moth may look so much like a bee or wasp that predators avoid it.

In mullerian mimicry, different species, all of which are poisonous, harmful, or distasteful, resemble one another. Although their harmfulness protects them as individual species, their similarity in appearance works as an added advantage. Potential predators can mores easily learn one common warning coloration. Viceroy and monarch butterflies are currently viewed as an example of mullerian mimicry (Solomon et al., 1996).

Mimicry appears to be a fairly common phenomenon among many plant and invertebrate species but it is considered a rarity among vertebrates. However, a complex and diversified array of coral snakes and non venomous mimics exist and has intrigued biologists for over a century (Roze, 1996). This phenomenon of coral snake mimicry only exists in the Americas.

While describing snakes found in the Academy of Natural Sciences of Philadelphia, Edward D. Cope noted in 1860 the curious fact that many venomous and non venomous snakes have quite similar patterns of red, black, and yellow bands (Figure 1). Several years later Alfred R. Wallace correctly interpreted the similarities in coral snake color pattern as mimicry (Roze 1996).

In this century there have been many objections to mimicry as a valid explanation for similarities among coral snakes and non venomous snakes with similar coloration. However, in 1981 Greene and McDiarmid summarized and clarified many of the objections concerning coral snake mimicry. They were able to show the incredible concordance of patterns between the poisonous coral snake (Micrurus) models and the non venomous snake mimics of the genera

Pliocercus and Lampropeltis (Figure 2). This influential work quieted much of the debate, however, some of the objections to mimicry in this system remain unexplored. One such objection is the occurrence of mimics in the absence of a model. Of all the objections to mimicry this is the least understood. Of particular interest is the system involving Micrurus (Coral snakes) and Lampropeltis (kingsnakes) in the United States. The genus Micrurus has a new world distribution from central South America to the southern United States (Figures 3 & 4). The genus Lampropeltis ranges from northern South America to southern Canada (Figure 5). This system is of interest because of the large area of allopatry of mimic and model in the United States. Lampropeltis maintains the mimicry pattern yet there are no local patterns to mimic. Examples of mᵑllerian mimicry have been hypothesized for many mimic/model complexes of coral snakes in southern Mexico to northern South America. The mimic/model system between Micrurus and Lampropeltis in the United States is considered an example of batesian mimicry. This is important to the theme of the arguments put forth because the mimics (Lampropeltis) are considered to be non venomous and thus not capable of maintaining the coral snake coloration through their own harmfulness.

One of the coral snake genera (Micruroides) also occurs in the United States but is not considered here in this study. It is particularly small (33-53cm) and is not considered to be a model for the significantly larger Lampropeltis (36-107cm)(Greene and McDiarmid, 1981; Roze, 1996). The species of Lampropeltis that are of specific concern are Lampropeltis triangulum, L. zonata, and L. pyromelana (for distributions see figures 6 - 8). L. calligaster and L. getulus are considered the basal taxon to the rest of the genera and do not exhibit any form of mimicry and therefore are excluded from discussion. It should also be noted that these two species are the largest of the genus (60-122cm) and therefore may not benefit from aposematic coloration. Other Lampropeltis which have mimic patterns that are excluded are L. mexicana, L. ruthveni, and

L. alterna. L. mexicana and L. ruthveni still occur in complete sympatry with a model and therefore are not discussed. Though L. alterna is allopatric to a coral snake model, it is also not considered as it is complicated by the fact that it may be now mimicking a second model: the rock rattle snake (Crotalus lepidus) (Markel, 1990).

Two hypotheses to explain this pattern of allopatric mimicry are proposed. The first possibility is that this does not constitute mimicry at all and the patterns are a result of similar selective forces resulting in a convergence of patterns (Gadow 1908, 1911; Brattstrom 1955). A second possibility is that allopatry in the mimic and model is a fairly recent event and that the persistence of mimicry in allopatry to the model is due to a combination of other selective forces and phylogenetic inertia. This hypothesis maintains that mimicry evolved in a common ancestor to the Lampropeltis that was sympatric with coral snakes. Other selective forces might maintain the mimic coloration including neutral selection, sexual selection, gene flow in mimic populations from areas of sympatry with the model to populations in allopatry, gene flow in predator populations from areas of sympatry with the model to populations in allopatry, some other adaptive significance of the ringed pattern such as camouflage, and migration of predators to and from model and mimic populations.

Non-mimicry hypothesis

As mentioned before Greene and McDiarmid (1981) were able to show that the numerous examples of geographic concordance between model and mimic is more than coincidence due to convergence. Of importance for consideration in this study is that within the United States, the patterns of Lampropeltis triangulum resemble Micrurus fulvius more closely in sympatry. In western Mexico, L. triangulum shows color pattern shifts in concordance with changes in the width of red bands and presence or absence of black spots in the red bands of other Micrurus. This

pattern of geographic pattern shifts in itself indicates that this is a mimicry system and not convergent patterns.

Phylogenetic Inertia hypothesis

In 1993 Edwards and Naeem reviewed three hypothetical relationships between an organismal trait and an environmental factor reconstructed on a phylogenetic tree (Figure 9). An example of "phylogenetic inertia" is depicted in figure 9c. This example illustrates phylogenetic inertia as the trait of interest (mimic coloration) developed in a common ancestor because of some given environment (sympatry with model) and persists in descendants after the hypothesized selection pressure has ceased to operate. It is important to note that because the "hypothesized selection pressure" is no longer operating, it does not mean that other selection pressures are not acting on that trait at the present. This is the difference between causal selection and maintenance selection. The argument in this case is the forces responsible for maintaining the color patterns of the mimic populations of Lampropeltis are not necessarily the selective forces that brought about the color patterns themselves.

Methods

Suitable phylogenies for Lampropeltis were obtained from Garstka (1982), Williams (1988) and Tanner (1953). The taxonomy at the subspecies level consists of several unresolved polytomys but does not distort any final discussion; relationships found were hypothesized to represent phylogenetic relationships. Binary states of "+" or "-" were assigned to each species or subspecies according to whether it is currently sympatric with a coral snake model and whether it displays the mimic color pattern. No attempt was made to take into account the variation in pattern.

1. Lampropeltis (Figure 10). Analysis of figure 10 indicates that the presence of a model in sympatry with this clade occurred sometime in its past and is indicated by the filled rectangle. This is reflected by the known formation and radiation of Lampropeltis in the Miocene somewhere in the tropical regions of Central America to Mexico. It is believed that coral snakes were present at that time having had a southern dispersal into that region (Holman, 1995; Roze, 1996). All of the species having a mimic coloration pattern fall into one monophyletic clade suggesting the genesis of the color pattern prior to this clade indicated by the filled oval. The gray squares represent taxa which have varying degrees of sympatry with the model. Gray ovals represent varying degrees of the mimicry patterns present. L. triangulum occurs in both sympatry and allopatry with a coral snake model and exhibits variation in mimic pattern. L. zonata and L. pyromelana are both completely allopatric to a model which is believed to be secondary to the formation of the mimic pattern. Finally, L. alterna also shows a secondary displacement from a coral snake model. Despite questionable mimic patterns which exist in some of the taxa, it is clear that the mimic pattern continues to persist in L. zonata, L. pyromelana and some L. triangulum despite the absence of a model. Thus it is hypothesized that mimicry only evolved once in this genus.

2. Lampropeltis triangulum (Figure 11). The various unresolved polytomys in figure 11 (Williams, 1988) represent groupings based on banding patterns. The groups depicted here are most likely artificial in their nature but is a monophyletic group as a whole. The first two polytomys in figure 11 are those subspecies found in the United States. One other subspecies, L. t. annulata, does occur in the U. S. but occurs sympatrically with Micrurus so its inclusion into another group is not important.

All of the subspecies represented here maintain a mimic color pattern although there is more variation found in populations of L. t. triangulum and L. t. multistrata, the two most northern populations of L. triangulum. Because all of the subspecies that are no longer sympatric with the

model represent the northern subspecies, it is unlikely this occurred independently six different times. However, because the phylogenies are not more resolved, allopatry is represented as six independent events.

3. Lampropeltis zonata and Lampropeltis pyromelana (Figure 12). L. zonata and L. pyromelana represent sister taxa and, presumably, their speciation occurred in the absence of a model. Neither species is sympatric to a coral snake model, yet, as indicated, they maintain their mimic pattern. One exception to this is L. z. herrerae which occurs on Todos Santos Island about 10 miles off shore of Baja California, Mexico. It lacks the red banding found in other related subspecies yet traces of red can still be commonly found. This is an interesting observation yet there is a strong possibility that genetic drift may be a strong influence on this small, isolated population.

It is evident from the dendrograms in figures 10-12 that mimic coloration arose once in the Lampropeltis very early in the genus' history. This is reflected in the persistence of the red, black and yellow colors throughout the genus with the exception of L. getulus and L. calligaster. Although the events leading up to the disjunction of Lampropeltis and Micrurus populations are unclear, it is clear that those populations of Lampropeltis that are allopatric to populations of Micrurus gained their coloration from an ancestor that was sympatric with Micrurus. The entire species groups of L. zonata and L. pyromelana and portions of the L. triangulum species group exhibit this pattern of maintaining aposematic coloration despite the absence of a coral snake model.

Other selective forces acting upon mimic coloration

The question then remains, "Why does mimicry persist in the absence of a model?" Establishing that bright warning coloration is a result of phylogenetic inertia only explains the persistence of mimicry over a short period of time. One would reasonably expect that aposematic coloration is meant to be seen and that if the primary protection of such coloration is gone then predation pressures would be expected to strongly select against such false signaling. Here other

explanations for the maintenance of bright colors in disjunction with a coral snake model are discussed.

One that is proposed here is that there is no or very weak selection against the coloration and therefore has not disappeared. This hypothesis does not seem very reasonable considering the purpose of the coloration itself. Even if disjunction between populations only occurred at the end of the last ice age (~10,000 ybp) predation pressures would be a strong selective force barring any other selection. Because this hypothesis is difficult to assess or test it is assumed here that this is not the case.

A second possibility is that this bright coloration is maintained by sexual selection. the suggestion here is that males or females or both prefer mating with brightly colored individuals. In the absence of other negative selection pressures this might seem reasonable; however, it is commonly accepted that most snakes, including coral and kingsnakes, have poor eyesight and that primary sex and species recognition is chemical in nature (Goin, and Goin, 1962).

A third hypothesis for the maintenance of mimicry in this system is the possibility that there is gene flow from areas where Lampropeltis and Micrurus are sympatric to populations of Lampropeltis that are allopatric to Micrurus. This model entails members of sympatric populations of Lampropeltis migrating out of the population and intergrading with allopatric populations. At first this seems unlikely due to the vast number of populations that are allopatric to the coral snake model coupled with the fact that these snakes are not known for long distance dispersals. In addition this seems improbable for the completely isolated populations of L. zonata and L. pyromelana. However, an inspection of a distribution map of L. triangulum with the number of red bands marked for different populations indicates a pattern that might be created from gene flow (Figure 13). The map illustrates how closely the number of red bands in L. triangulum (~15-18) match the number of black bands (used here as a surrogate for how closely the patterns match) of Micrurus fulvius (~13-18) in areas of sympatry in the southern U. S. As

one traces the number of red bands in L. triangulum northward a clinal pattern emerges. The number of bands steadily increase from ~18 in Texas and Florida up to ~40 in southern Canada. The suggestion here is that gene flow has the strongest influence closer to those areas where the model and mimic occur together, thus maintaining a lower number of red bands.

A related hypothesis is that there is gene flow in predator populations from areas where there are models to areas were there are no models. The same map (Figure 13) can be invoked to illustrate this possible phenomenon. However, the difference here is that predators (primarily birds of prey) that are closest to the model populations would be maintaining a mimic pattern in Lampropeltis triangulum that is close to that of patterns in areas of sympatry with the model. This is underscored by the known innate avoidance of many predatory bird species to coral snake colors. Greene and Pyburn (1973) suggested that an important part of the mimicry maintenance is the innate avoidance of brightly banded snakes by potential coral snake predators (Gehlbach, 1972; Smith, 1975 and 1977). They proposed that the tendency to attack colorful coral snakes varies between individual predators, and it may be genetically determined. Since attacks on coral snakes are frequently fatal, predators who innately tend to avoid them would have better chances to survive and reproduce.

Another possibility for the maintenance of the mimicry pattern has been proposed by several authors (Pough, 1976; Goodman and Goodman, 1976; Emsley, 1966; Grobman, 1978; Zweifel, 1952). The suggestion is that the ringed pattern of these coral snake mimics serves some other adaptive purpose other than warning coloration. Grobman (1978) pointed out that many snakes have a ringed pattern that most likely serves in a cryptic capacity through a disruptive and illusory effect. The banding pattern not only allows the snake a certain amount of background matching but when the snake moves at a fast pace the pattern looks like one color and when it stops abruptly the pattern breaks up and may be hard for the predator to find. Both Grobman (1978) and Pough(1976) argue that the colored rings in the Lampropeltis in areas where there are no

models gives them an extra advantage in that it may serve the same function of crypsis with the advantage of fooling predators that have color vision. Another interesting observation made by Goodman and Goodman (1976) suggested that some populations may want to be seen. They watched an individual snake (L. zonata) sit out in very conspicuous spots at various points along a creek. Eventually a pair of Dusky Flycatchers saw the snake and attacked it. The snake apparently used the frequency of attacks over a period of an hour to locate the nest the birds were protecting and devoured the eggs. This use of aposematic coloration to engage in a game of "hot and cold" for food was termed thelgosematic coloration by the authors. This hypothesis is not resolved but experiments are suggested later that may shed some light on the subject.

Finally, a last hypothesis considered here is that mimicry is maintained by migration of predators. Pough (1976) indicated that the mimicry coloration in allopatric populations of Lampropeltis had to serve some other function than a warning because, if not, then predatory pressures would eliminate the pattern. This hinges on the notion that there is no reinforcement of the innate avoidance behavior (see discussion above) found in many predators in those areas. However, the primary predators of Micrurus and Lampropeltis (and larger snakes in general) are predatory birds of prey. Many of these birds migrate for the winter and there is the possibility that reinforcement for an innate avoidance may occur in areas where there is a model and therefore is present when they migrate back into areas where there are no models. A review of diets and migration patterns of the hawk species that occur in the United States yielded Table 1 and Figure 14 (Clark and Wheeler, 1987; Keast and Morton, 1987). A review of Table 1 reveals five common avian predators that include snakes in their diet. All of the species listed also have a southward migration during the winter to warmer areas. The Red-shouldered Hawk and the Red-Tailed Hawk do not migrate as extensively as the others but the thing that they all have in common is that during the winter, all or portions of their populations can be found in areas where there are several coral snake models. This suggests that they are exposed to these models and that there may be some

level of innate avoidance present. This possibility has not been given much attention in the literature but the patterns suggest that it should.

Experiments to test hypotheses

Despite the fact that some of the hypotheses concerning the maintenance of mimicry coloration can be dismissed, there are still several that cannot. In this section some suggestions are made as an approach one might take to test these hypotheses.

The gene flow models with respect to mimic and predator populations are probably the hardest to test. Because of the inability to handle this subject in its entirety here, a general approach is suggested. The challenge here is two-fold. First one must be able to assess the level of selection acting on populations with the mimic coloration that do not occur sympatrically with a model. Next the amount of gene flow between populations has to be assessed. This approach is compounded by the theories purported for how many migrants are required to maintain certain traits in a population. If one can show that selection pressures are greater than what can be overcome by gene flow then this model is suspect. L. triangulum would be the only logical place to look for this phenomenon since there is a large continuous population that only partially overlaps a coral snake population.

To test the hypotheses regarding cryptic/conspicuous coloration versus innate avoidance in migratory predators, an approach is recommended that has been used in other areas. Brodie and Janzen (1995) were able to utilize a fairly simple technique in Costa Rica using plasticine models (Figure 15). They used these models in transects and were able to establish which models were attacked and by what kind of predator. It was determined that there existed an avoidance of bicolor and tricolor patterns in snakes by avian predators (Figure 16). Application of this technique in various populations can determine the level of innate avoidance in those predators suggested earlier. Of interest is the fact that the predators seemed to avoid the bicolored model as

well suggesting that for some predators that there is a generalized pattern that might be avoided and thus would suggest that the generalized patterns found in the northern U. S. are still serving as warning colorations.

Discussion

The mimicry system has not been completely worked out from a biological point of view but there is little doubt that it exists. The mimicry found among coral snakes and non venomous snakes in color patterns is truly unique in the vertebrates. It has produced many challenges to the ideas held about mimicry but it also provides some unique perspectives on how selective forces can work on populations differently. Herein discussed in this paper are several ways that selection can act. It is likely that these hypotheses are not mutually exclusive and probably work in complex ways to maintain the mimicry coloration. This work attempts to use phylogenetic background material to establish the origin of the mimic trait specifically in <u>Lampropeltis</u>. It is also meant to establish that the mimic coloration was established in a common ancestor. This information sets the stage for the possibility of "phylogenetic inertia". Phylogenetic inertia may be an underappreciated phenomenon due to the difficulty of mapping environmental traits and characteristics on phylogenetic trees. This can be complicated at any level, for instance, presence or absence of a given environment or trait may not be known, or the phylogeny used to in analysis may have serious flaws that would affect results. However, finding these patterns can lead to a more productive search for selective forces acting on populations.

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A

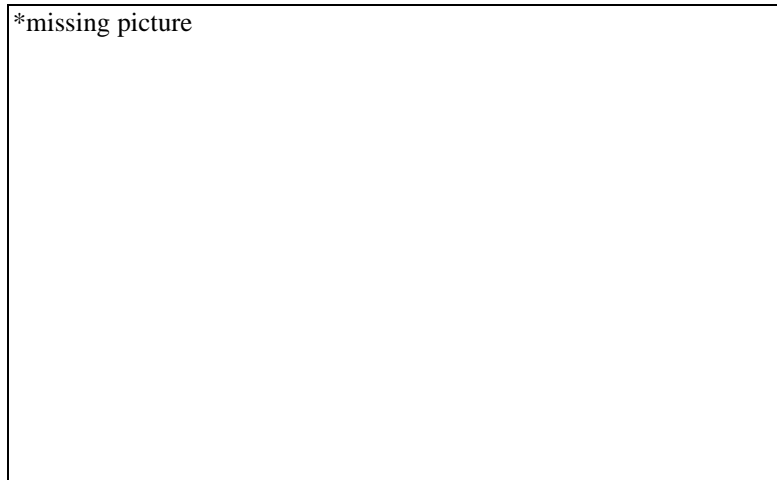**B**

*missing picture

Figure 1: Examples of typical (A) kingsnake (<u>Lampropeltis</u>) and (B) coral snake (<u>Micrurus</u>) color patterns. Examples used are (A) <u>Lampropeltis</u> <u>triangulum</u> <u>annulata</u> and (B) <u>Micrurus</u> <u>fulvius</u> <u>fulvius</u>.
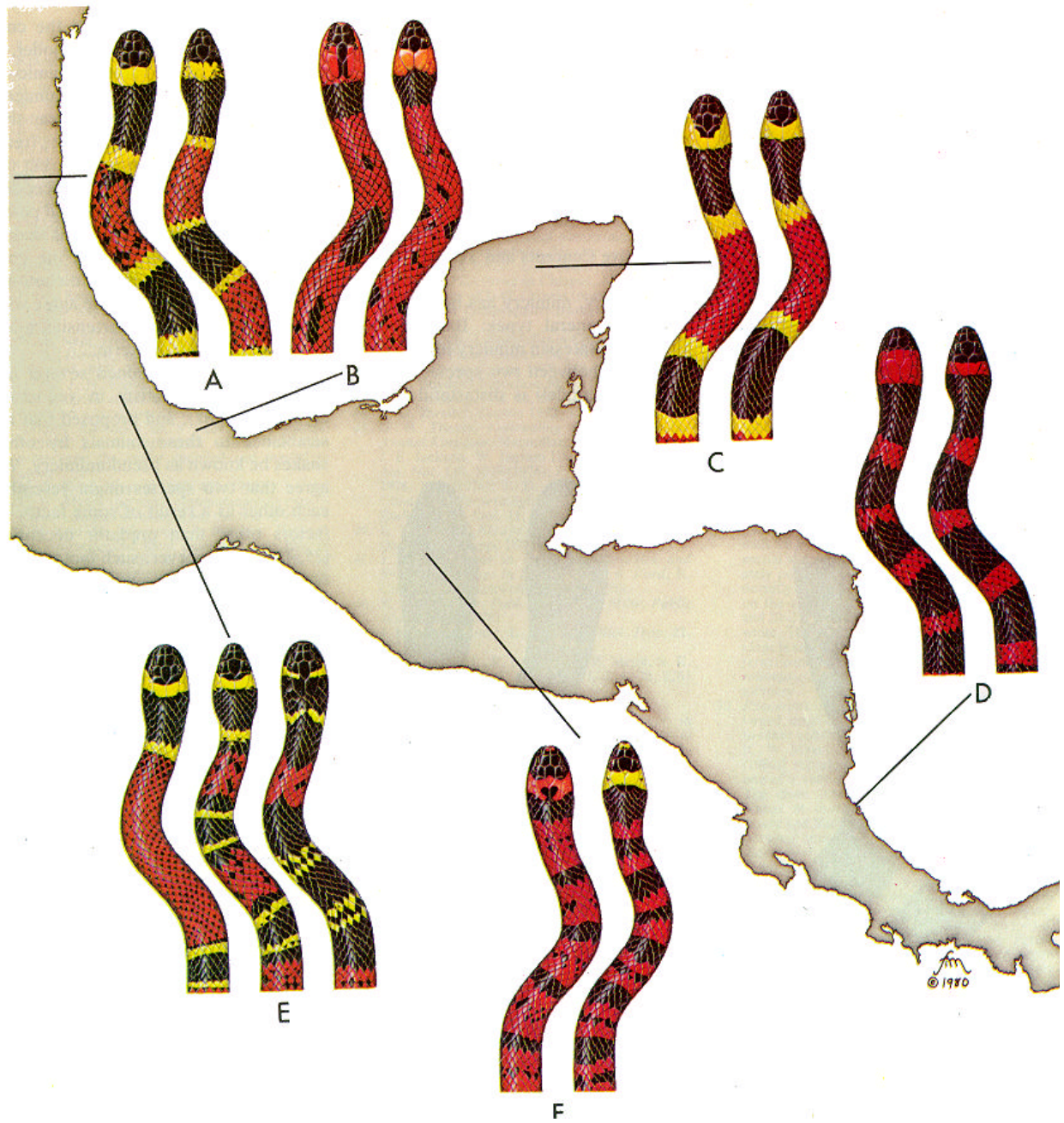
Figure 2: Geographic color pattern variation in rear-fanged colubrid snakes of the genus Pliocercus in relation to sympatric front-fanged snakes of the genus Micrurus. The presumed dangerous models, on the left in each set, are (A) M. fulvius, (B) M. limbatus, (C) M. diastema, (D) M. mipartitus, (E) M. diastema, and (F) M. diastema. In (E), the center snake is Pliocercus, and the right snake is M. elegans (Greene and McDiarmid, 1981).
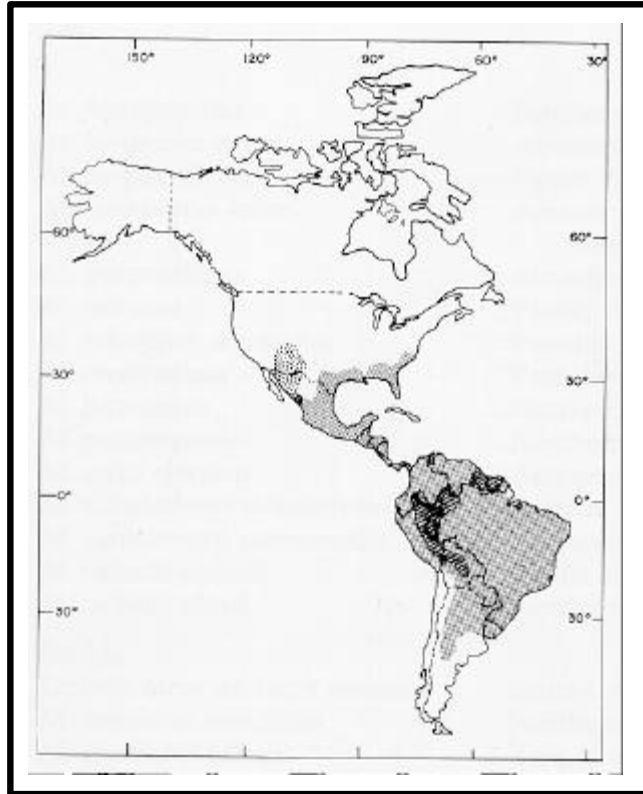
Figures 3 : Distribution of coral snakes (genus <u>Micrurus</u>, <u>Leptomicrurus</u>, and <u>Micruroides</u>) in the New world (Roze, 1996).
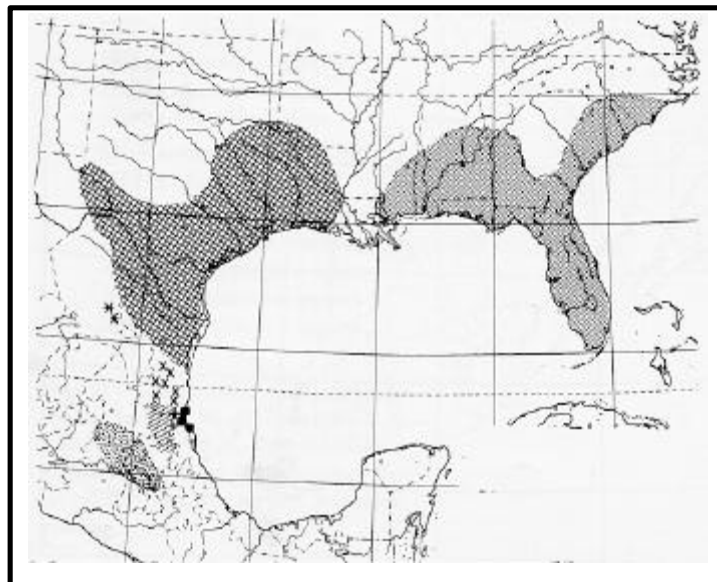

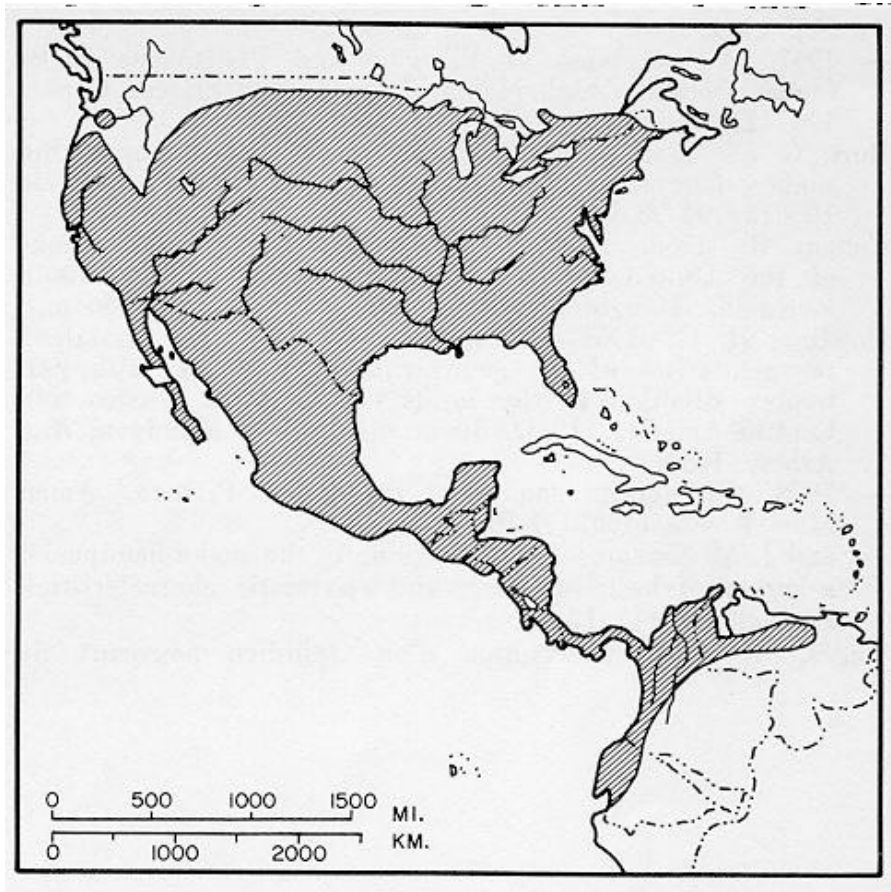Figure 4: The distribution of <u>Micrurus</u> in the United States (Roze, 1996).

Figure 5: Geographic distribution of the genus <u>Lampropeltis</u> (Blaney, 1973).

1. *Lampropeltis triangulum triangulum*
2. *L. t. abnorma*
3. *L. t. amaura*
4. *L. t. andesiana*
5. *L. t. annulata*
6. *L. t. arcifera*
7. *L. t. blanchardi*
8. *L. t. campbelli*
9. *L. t. celaenops*
10. *L. t. conanti*
11. *L. t. dixoni*
12. *L. t. elapsoides*
13. *L. t. gaigeae*
14. *L. t. gentilis*
15. *L. t. hondurensis*
16. *L. t. micropholis*
17. *L. t. multistrata*
18. *L. t. nelsoni*
19. *L. t. oligozona*
20. *L. t. polyzona*
21. *L. t. sinaloae*
22. *L. t. smithi*
23. *L. t. stuarti*
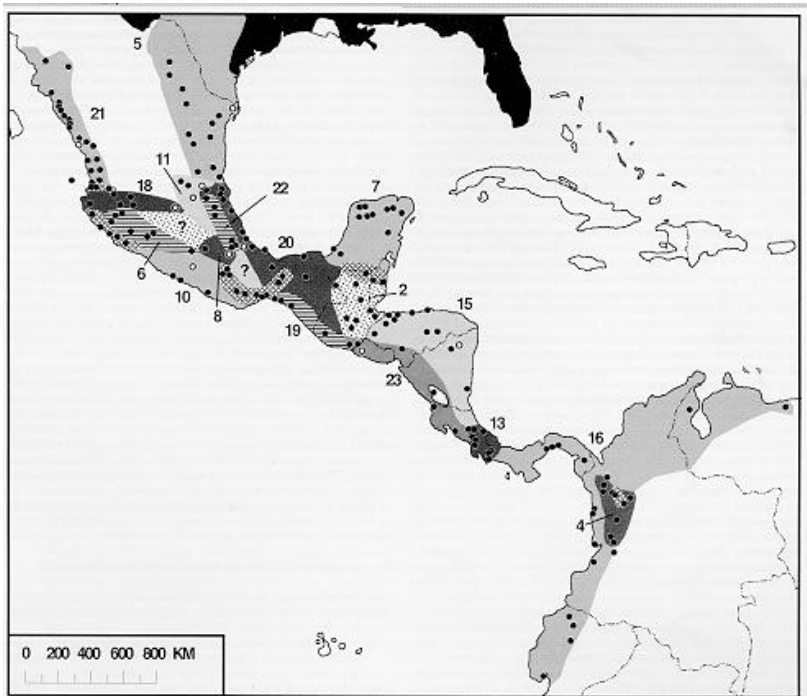24. *L. t. syspila*
25. *L. t. taylori*
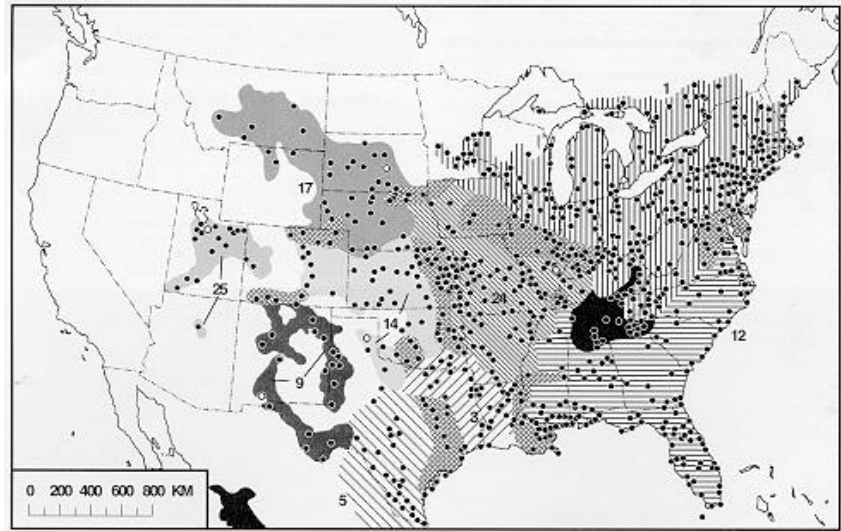
Figure 6: Distribution of <u>Lampropeltis triangulum</u> in the United States, Mexico, Central America, and northern South America. Type-localities are indicated by circles, other localities are marked with dots. Stars mark fossil localities. The black areas in the second map are included in the first map (Williams, 1994).
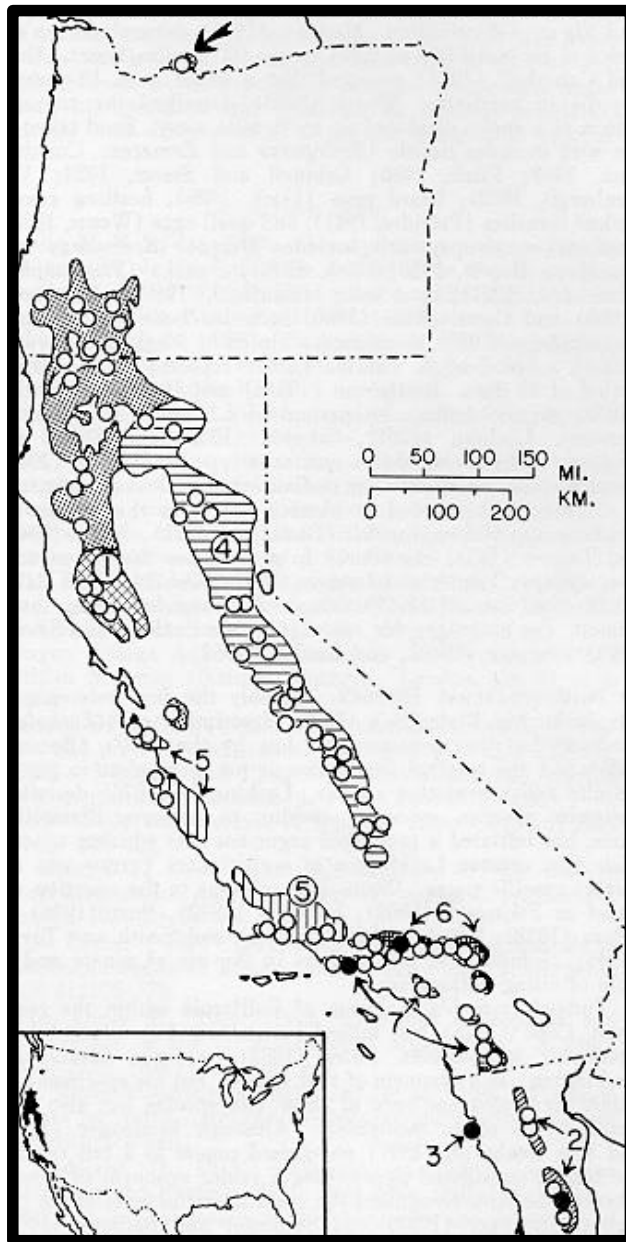
Figure 7: Distribution of <u>Lampropeltis</u> <u>zonata</u>. Solid symbols mark type-localities; open symbols indicate other localities. Areas of intergradation are stippled (Zweifel, 1974).

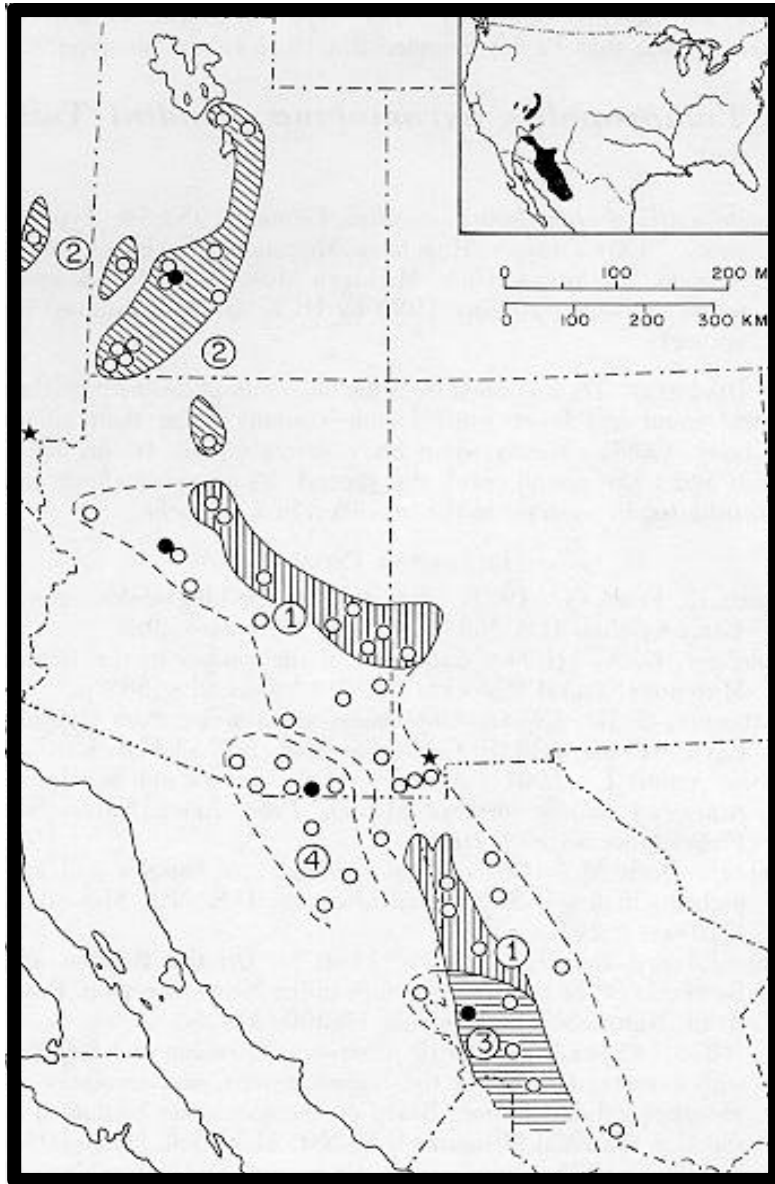Figure 8: Distribution of <u>Lampropeltis</u> <u>pyromelana</u>. Shaded areas are presumably continuous range; symbols within broken lines mark disjunct montane populations. Solid circles mark type-localities; open circles indicate other localities. Stars indicate Quaternary fossil sites (Tanner, 1983).
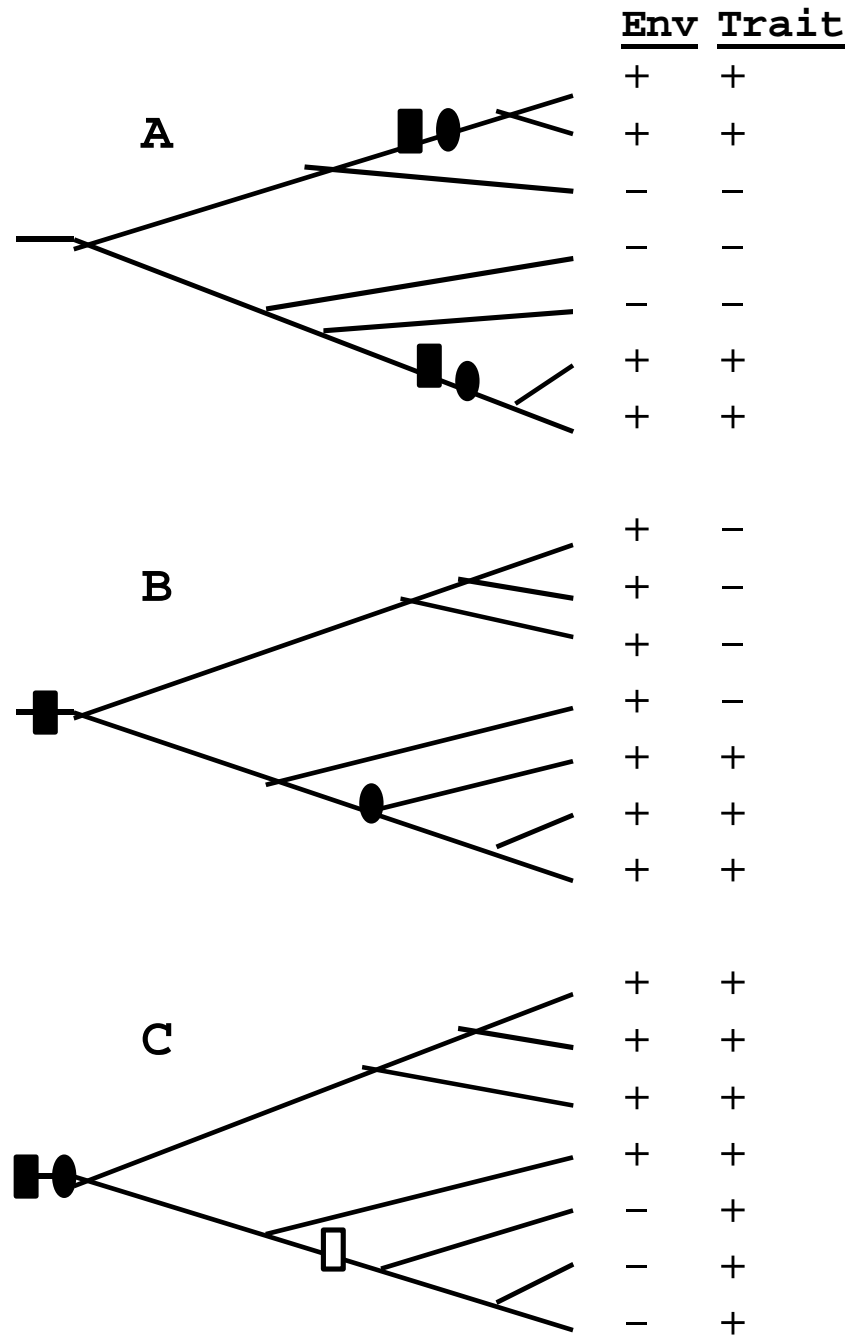
Phylogenetic Patterns

	Env	Trait
A	+	+
	+	+
	−	−
	−	−
	−	−
	+	+
	+	+
B	+	−
	+	−
	+	−
	+	−
	+	+
	+	+
	+	+
C	+	+
	+	+
	+	+
	+	+
	−	+
	−	+
	−	+

Figure 9: Three hypothetical relationships between an organismal trait and an environmental factor reconstructed on a phylogenetic tree. A "-" or "+" signifies the presence or absence of a trait or hypothesized selective environment, repectively, for that taxon. Solid ovals and rectangles represent the inferred origin of the trait or selective environment, respectively; the open rectangle in C represents the inferred loss of the selective environment. (A) A case of coincidental invasion of the selective environment and origin of the trait. (B) A situation in which the invasion of the hypothesized selective environment preceeds the inferred origin of the trait. (C) A case of "phylogenetic inertia," in which the trait of interest persists in descendants after the hypothesized selection pressure has ceased to operate (open rectangle) (Edwards and Naeem, 1993).
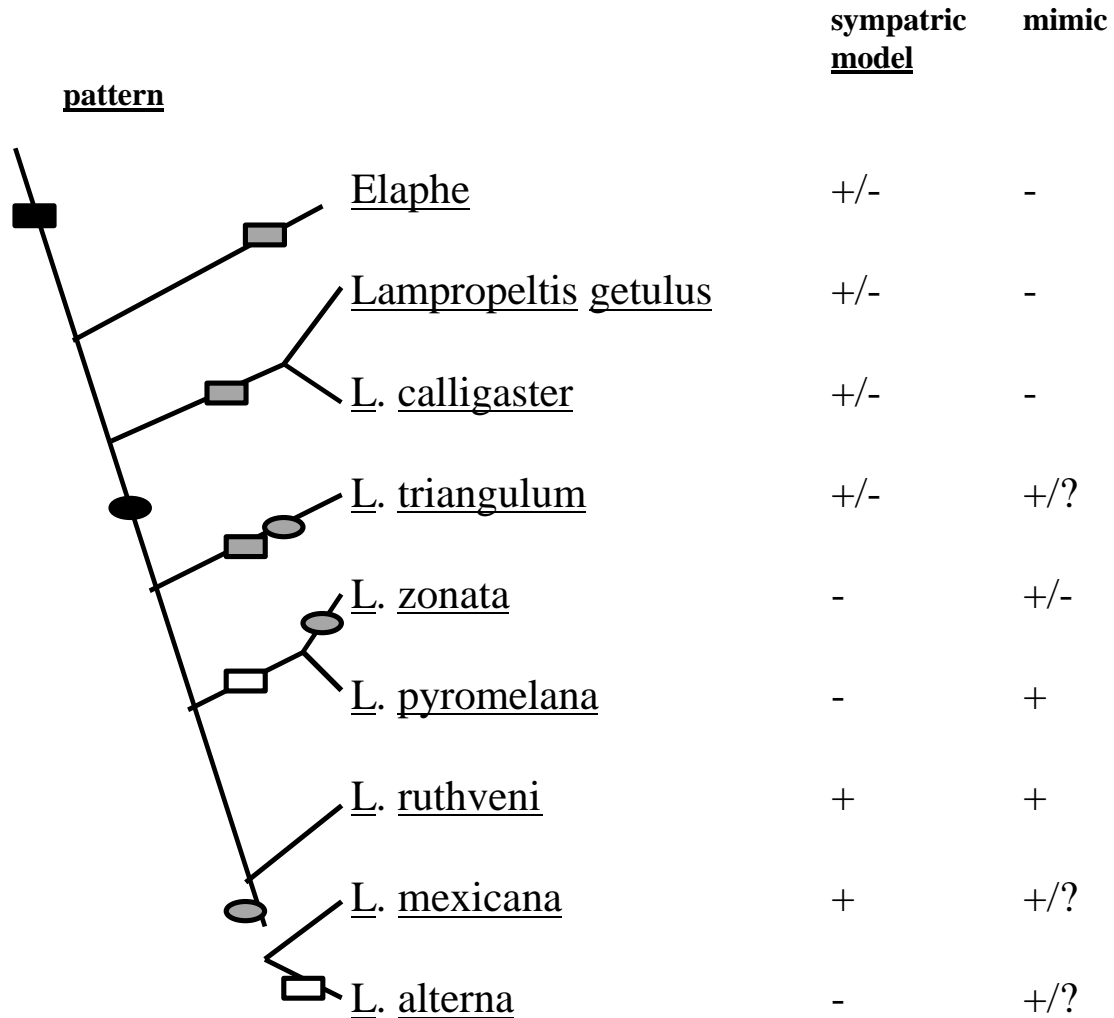
pattern

	sympatric model	mimic
Elaphe	+/-	-
Lampropeltis getulus	+/-	-
L. calligaster	+/-	-
L. triangulum	+/-	+/?
L. zonata	-	+/-
L. pyromelana	-	+
L. ruthveni	+	+
L. mexicana	+	+/?
L. alterna	-	+/?

Figure 10: Phylogenetic hypothesis of the genus lampropeltis and an outgroup genus Elaphe. At the end of each branch a "-" or a "+" sign indicate the presence or absence of a coral snake model and the mimic pattern, respectively. Question marks indicate the uncertainty of the trait in some of the members of that species. A "+/-" indicates that both conditions are true in that species. Open and solid ovals indicate, respectively, inferred loss and gain of mimic coloration along that branch. Gray ovals indicate variation within that branch. Open and solid rectangles indicate, respectively, inferred allopatry or sympatry with a coral snake model. Gray rectangles indicate variation within that branch.

Lampropeltis triangulum

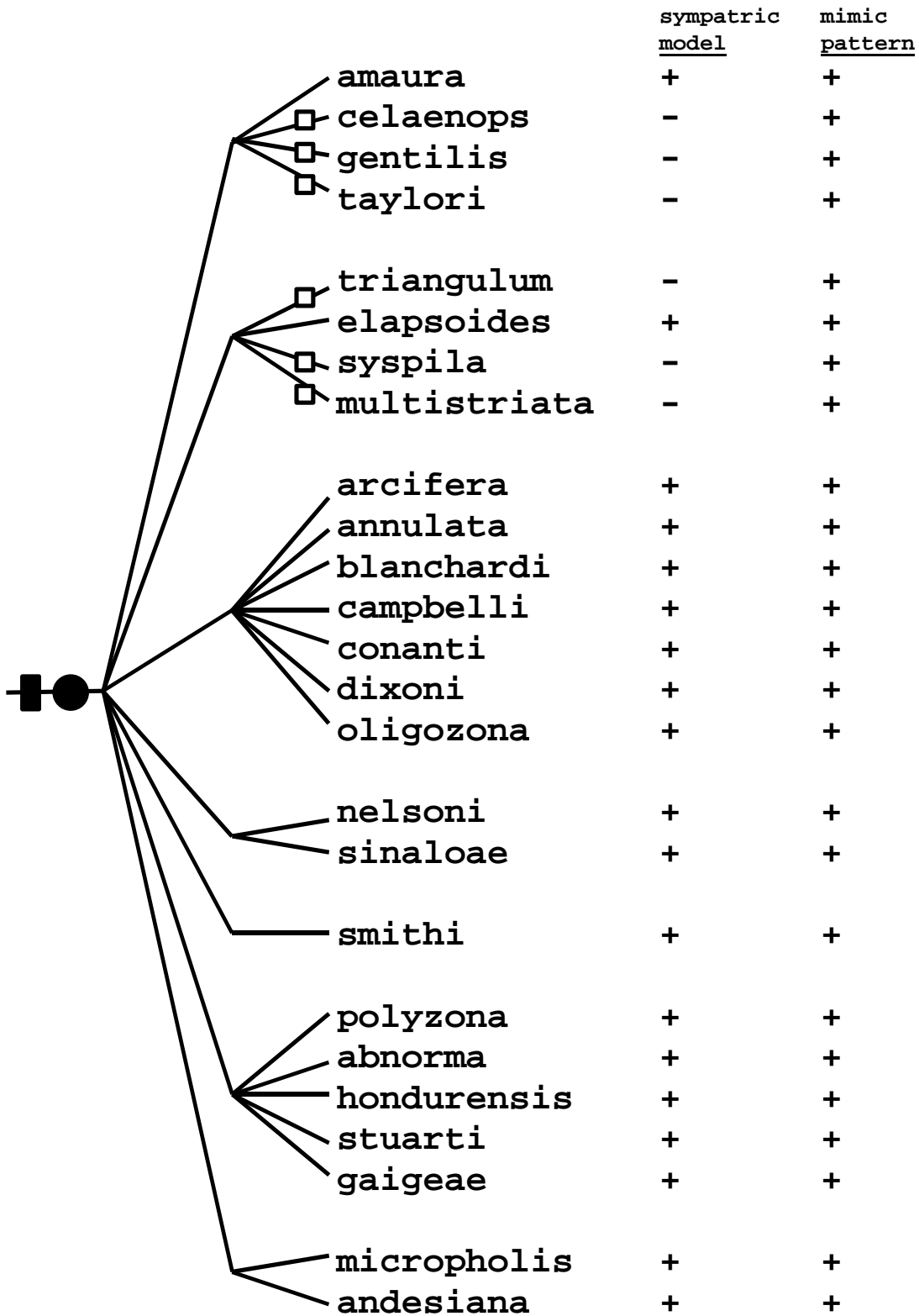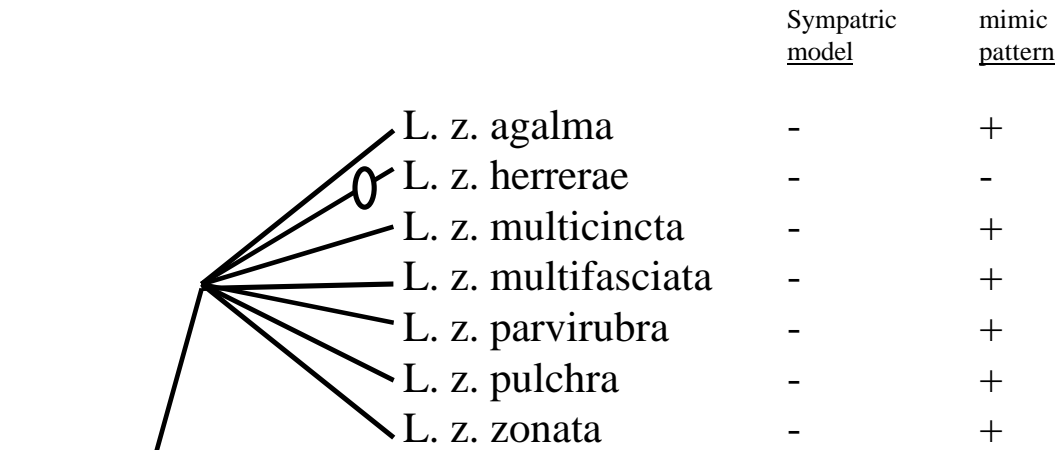|	sympatric model	mimic pattern
amaura	+	+
celaenops	−	+
gentilis	−	+
taylori	−	+
triangulum	−	+
elapsoides	+	+
syspila	−	+
multistriata	−	+
arcifera	+	+
annulata	+	+
blanchardi	+	+
campbelli	+	+
conanti	+	+
dixoni	+	+
oligozona	+	+
nelsoni	+	+
sinaloae	+	+
smithi	+	+
polyzona	+	+
abnorma	+	+
hondurensis	+	+
stuarti	+	+
gaigeae	+	+
micropholis	+	+
andesiana	+	+

Figure 11. Phylogenetic hypotheses for Lampropeltis triangulum. See figure 10 for explanation.

Lampropeltis zonata

	Sympatric model	mimic pattern
L. z. agalma	-	+
L. z. herrerae	-	-
L. z. multicincta	-	+
L. z. multifasciata	-	+
L. z. parvirubra	-	+
L. z. pulchra	-	+
L. z. zonata	-	+

Lampropeltis pyromelana

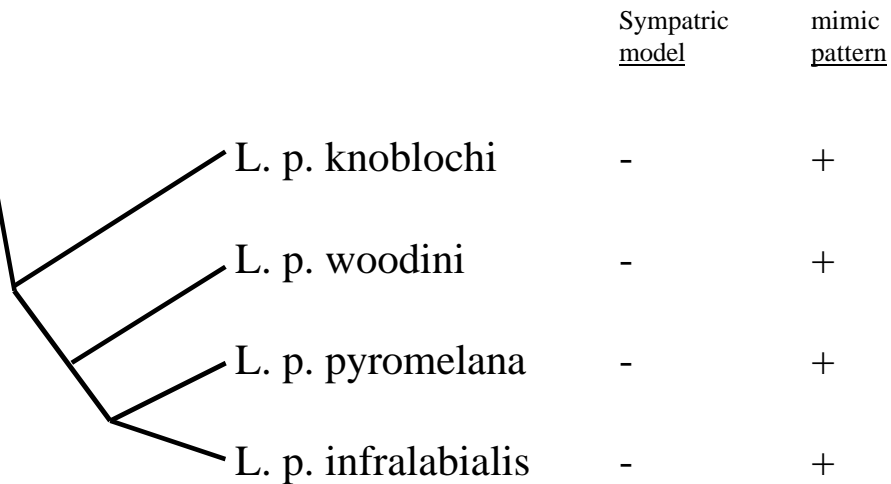|	Sympatric model	mimic pattern
L. p. knoblochi	-	+
L. p. woodini	-	+
L. p. pyromelana	-	+
L. p. infralabialis	-	+

Figure 12: Phylogenetic hypotheses for Lampropeltis zonata and L. pyromelana. See figure 10 for explanation. Phylogenetic hypotheses come from Markel (1990) and Garstka (1982).

35.8(5)   37.8(32)   37.4(37)   35.4(33)   36.6(37)   32.8(86)   25.3(4)   20.6(5)

38.9(16)   25.4(7)   17.4(15)   17.6 (18)

36.7   57.1(7)   36.1(13)   37.4   37.2(55)   28.2(26)   35.5(19)   16.0(23)

40.7(3)   41.0(49)   35.3(26)   42.6(10)   35.3(16)   36.8(28)   15.7(6)   15.4(46)

38.0(7)   36.4(14)   16.6(66)

42.3(11)   36.8(4)   37.2(5)   32.7(10)   34.8(27)   17.3(7)   16.4(21)

36.3(9)   45.3(3)   33.4(9)   30.3(37)   22.7(10)   24.4(5)   32(1)   15.4(12)

41.0(2)   38.0(7)   41.4(21)   28.3(16)   20.8(27)   18(1)   18(1)   16.6(33)

33.3(6)   22.5(36)   23.0(29)   22.2(6)   18.5(2)   15.6(106)   17.1(7)

28(1)   27.2(9)   25.6(5)   25.7(32)   24.4(63)   24(1)   24.3(6)   15.8(21)   15.8(34)   17.7(6)   17.0(29)   18.1(15)

26.4(8)   26.7(15)   28.4(7)   25(1)   26.0(4)   20(1)   22.5(2)   20.5(17)   16.8(5)   18.0(15)

28(1)   27.3(7)   26.5(6)   21.7(7)   22(1)   20.5(2)

26.3(3)   28.4(36)   25.9(35)   25.5(13)   22(1)   17(1)

26(1)   23(1)

29.1(15)   23.8(5)

28.7(18)   28(1)

31.0(3)

Scale

miles
100 200 300 400 500

kilometers
200 400 600 800

Table 1: A list of common birds of prey and migration ranges (Clark and Wheeler, 1987).

Avian Predator	Wintering range	Summer range
Red-Shouldered Hawk	Eastern US, *Florida/Mexico	Eastern US
Broad-Winged Hawk	South and Central America	Eastern US
Swainson's Hawk	South America, Florida	Central and Western US
Red-Tailed Hawk	US, Mexico, *South US	North America
American Kestrel	South US - Central America	North America

* Northern population wintering spots
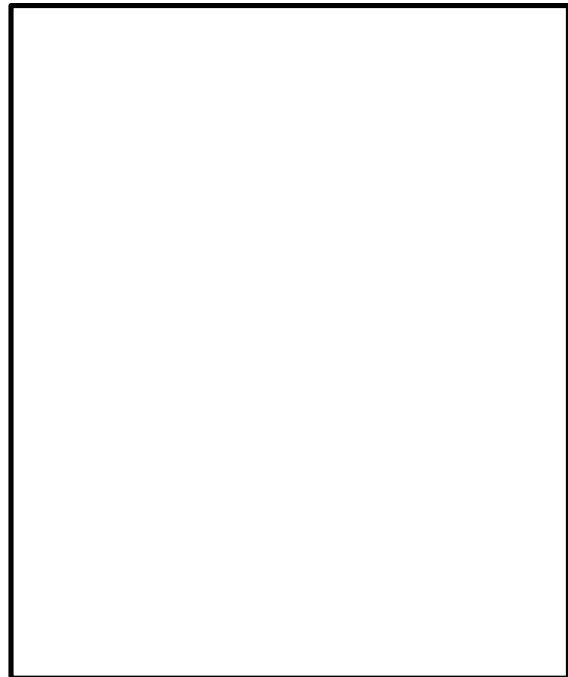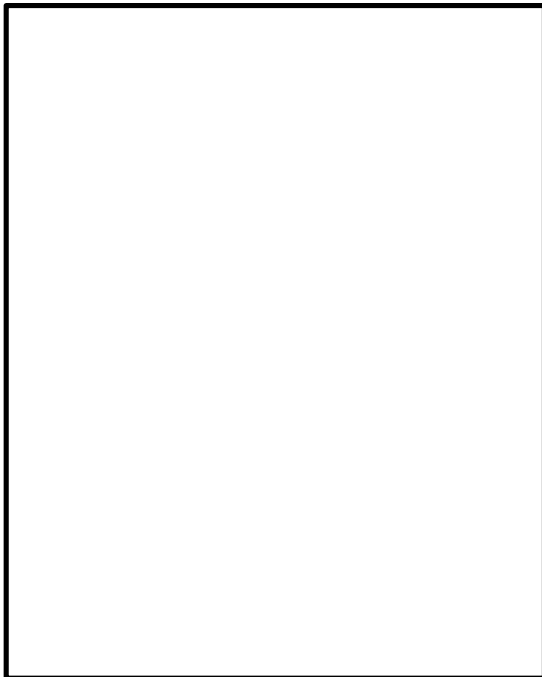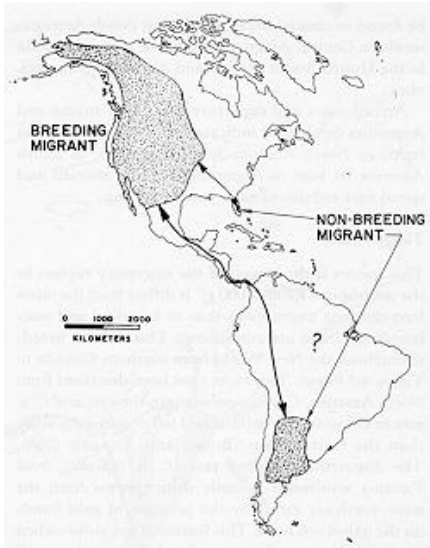
Swainson's Hawk   Broad-Winged Hawk

Figure 14: Examples of migration route of Swainson's Hawk and the Broad-Winged Hawk.
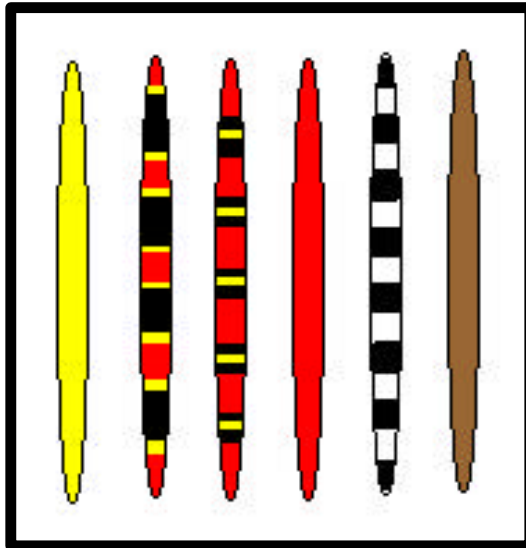
Figure 15: examples of plasticine model patterns that can used in experiments to assess innate avoidance by predators in a given area.
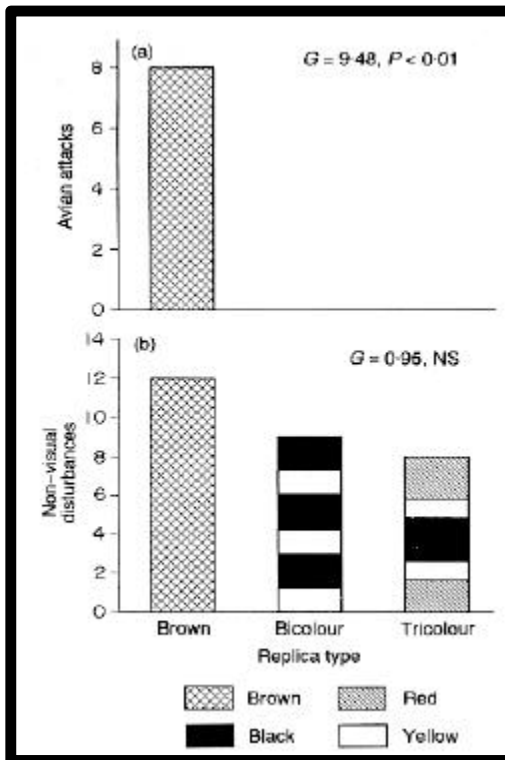

Figure 16: Number of avian attacks (a) and non-visual disturbances (b) of different replica types. The patterning of bars in (b) denotes the color pattern of each replica type (Brodie and Janzen, 1995).