The Strange Case of Mimicry in the New World Coral Snakes:

A Review

by

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Running Head: CORAL SNAKE MIMICRY

Abstract

The coral snakes of the New World comprise a mimetic group of highly venomous, mildly venomous, and nonvenomous species of the families Elapidae and Colubridae. At various times the highly poisonous, the mildly poisonous, and the nonvenomous species have been suggested to be the models, and have also been suggested to be the mimics. Greene & Pyburn (1973) have suggested that despite textbook treatments which have implied that the problem of coral snake mimicry has been more or less resolved, this is not the case. This paper reviews the theoretical and empirical contributions to the literature of coral snake coloration and examines the plausibility of the various proposed causal mechanisms. Natural selection operating on predators is proposed as the mechanism which is most likely to be responsible for the evolution of and maintenance of coral snake mimicry.

The Strange Case of Mimicry in the New World Coral Snakes:

A Review

Since the publication of a paper by Cope in 1860, the mimetic complex of the coral snakes of the New World has been the subject of much discussion and little agreement among herpetologists. Greene & Pyburn (1973) suggested that despite textbook and popular treatments which have implied that the problem has been more or less resolved (cf Allee et al., 1949; Cott, 1957; Edmunds, 1974; Klopfer, 1962; Owen, 1980; & Wickler, 1968), the problem remains unsolved. However, despite the importance of coral snake mimicry for biological theory [Wickler (1968) coined the term Mertensian mimicry to account for coral snake coloration], there have been no major theoretical papers on the subject since Greene & Pyburn's in 1973. The purpose of this paper is to review theoretical and empirical contributions to the coral snake mimicry literature to date, to comment on the plausibility of the various causal mechanisms which have been suggested, and to propose that natural selection operating upon predators of coral snakes is the mechanism which is most likely to be the agent responsible for the evolution of coral snake coloration.

The Coral Snakes of the New World

A group of venomous and nonvenomous snakes of the New World are called the "coral snakes". They comprise about seventy-five species in eighteen genera (Wickler, 1968). These snakes are typically characterized by coloration with transverse bands (annulations) of bright red, yellow or white, and black (Smith, 1975). Some of the snakes are very poisonous Elapidae (genera Micrurus, Micruroides, and Leptomicrurus), some are slightly poisonous Colubridae (Erythrolamprus spp.), and others are harmless Colubridae (Lampropeltis spp.) (Edmunds, 1974). Wickler (1968), however, pointed out that in coral snakes the family tree is no guarantee of harmlessness or noxiousness. "The same sub-family may contain poisonous and non-poisonous snakes... similarity in colour is therefore no indication of kinship and is not determined by ancestry. Conversely, difference in coloration is no argument against relationship" (p. 114).

All snakes with a coral pattern have been called "coral snakes", although the name is most commonly associated with the very venomous elapid genera Micrurus, Micruroides, and Leptomicrurus. Because the coral pattern occurs in these snakes regardless of habitat, and because the pattern occurs in colubrids primarily where they are sympatric with elapid coral snakes, the very venomous elapids have been called "true" coral snakes (cf

Wickler, 1968). In order to avoid the value-laden connotations of the word "true" (it does, after all, imply that the other snakes are "false", and hence must be the mimics), the elapid coral snakes will be referred to as very venomous or deadly venomous coral snakes. Coral snakes of the family Colubridae will be called colubrid coral snakes. The more general term "coral snake" will be used to refer to all snakes with a coral pattern.

The Very Venomous Coral Snakes

Of the highly poisonous snakes of genera _Micrurus_ and _Micruroides_, two species with distinctive red, black, and yellow bands are known in the southeastern and southwestern United States, (Conant, 1975; Behler & King, 1979). In Mexico a variety of species with variable coloration are found; in some Mexican species coloration is not the typical red, black, and yellow that most Americans associate with coral snakes (Schmidt, 1933). A variety of species of very poisonous _Micrurus_, _Micruroides_ and _Leptomicrurus_ are found in Central and South America, and show considerable variability in coloration (Dunn, 1949, 1954).

The Colubrid Coral Snakes: A Mimetic Complex?

Most colubrid snakes are nonvenomous, but a few species are poisonous. Colubrids are found throughout the range and outside the range of the very venomous coral snakes (Conant, 1975; Behler & King, 1979). A number of colubrids which are sympatric with very venomous coral snakes share their "coral" coloration throughout at least part of the range of sympatry and have been considered to be Batesian or Mullerian mimics. Large number of species of models and presumed mimics have overlapping ranges, especially in tropical areas, resulting in a potentially very confusing and complicated array of mimetic relationships; this is exacerbated by a general lack of knowledge of the relative abundance, ecology and behavior, and sometimes even the typical coloration, descent, and morphology of many species.

Colubrid species which are presumed to be coral snake mimics are colored like very venomous coral snakes. The red, black, and yellow or white bands which are found in the models are typically present in the presumed mimics. The relative width and adjacent colors of the bands may be different in mimics and models (Mertens, 1956), and annulations, which completely encircle the very venomous coral snakes, may or may nor extend across the ventral surfaces of colubrid coral snakes. The "match" of mimics and models often varies with geographical area and may be excellent in some areas and poor in others.

Coral snakes "on the move" are almost impossible to identify, and even experts have been known to misclassify specimens (Wickler, 1968). For example, the very venomous coral snake of the eastern United States, Micrurus fulvius, has a black head and a recurring "yellow-black-yellow-red" pattern. The milk snake Lampropeltis doliata triangulum is a presumed mimic with a yellow head and a "red-black-yellow" pattern. Upon close inspection these two snakes can be told apart, but the resemblance is very striking. It is not hard to imagine that a predator might have trouble discriminating the two species and might, if it tends to avoid very venomous coral snakes, also tend to avoid colubrid mimics. This point, however, has been a bone of contention in the coral snake mimicry controversy, as it has been argued that a predator would be unlikely to survive the bite of a very venomous coral snake, and would therefore not be around to avoid any mimics. Brattstrom (1955) and Wickler (1968) have argued that for this reason very venomous coral snakes cannot be the models in the coral snake mimetic complex.

Physical and Behavioral Characteristics of Coral Snakes

Adult very venomous coral snakes (genera Micrurus, Micruroides and Leptomicrurus) range in size from about 30 cm to over 1 m (Conant, 1975; Behler & King, 1979). The head is blunt. These snakes tend to be thin and are cylindrical in shape and of uniform thickness, except for the tail; that is, the head is the same width as the body (cf Wickler, 1968, p. 117). Coloration consists of bright, highly contrasting tricolor or bicolor bands (annulations) of red, black, and yellow (or sometimes white). Bands typically extend across ventral as well as dorsal surfaces. It has been argued that this type of coloration is disruptive and concealing (Brattstrom, 1955; Greene & Pyburn, 1973) and conversely, that it is warning coloration (Hecht & Marien, 1956; Wickler, 1968).

Until recently, coral snakes were considered to be nocturnal (Dunn, 1954; Brattstrom, 1955), but are now considered to be somewhat active during the day (Neill, 1957; Smith, 1969; Wickler, 1968). A possible reason for this confusion about the diurnal patterns of coral snakes may simply be that different species are active at different times of day or in particular weather conditions (Conant, 1975; Behler & King, 1979).

Coral coloration is found in many different habitats, and so does not seem to be an adaptation for any particular environment; neither does it seem to be associated with daily activity patterns or diet (Wickler, 1968). In colubrid coral snakes the pattern does seem to occur primarily in areas in which very venomous coral snakes are found, and to match the peculiarities of various populations of very venomous coral snakes (Emsley, 1966; Hecht & Marien, 1956).

Very venomous coral snakes are not considered to be especially pugnacious, although they have been known to bite when picked up (Greene & Pyburn, 1963; Wickler, 1968). Colubrid coral snakes, especially the moderately venomous species of Lampropeltis are much more likely to bite (Edmunds, 1974). Gehlbach (1972) reported "self-mimicry" in very venomous coral snakes; when disturbed by being touched, these snakes tend to hide their heads beneath a body coil and raise and even "strike" with their tails. During this "self-mimicry", they do not bite.

Very venomous coral snakes and many colubrid coral snakes are ophiophagous (snake-eating). Their relationships with prey are not well known. Predation has been observed by birds (Pough, 1964; Smith, 1969), and presumably predation by mammalian, reptilian, and even amphibious predators occurs (Brattstrom, 1955; Wickler, 1968).

Mimetic Systems

It was early discovered that some coral snakes were poisonous and that others were not (Wickler, 1968). Cope (1860, cited in Dunn, 1954) apparently suspected a typical Batesian mimicry complex. Batesian mimicry is the resemblance of a palatable mimic to a model which is in some way noxious or unpalatable; it has been well documented in a variety of different orders of animals, and to a lesser extent in plants (cf Wickler, 1968). The familiar example of palatable Viceroy butterflies, which mimic noxious Monarch butterflies is an example of Batesian mimicry (Brower, 1969). The model typically "advertises" its noxiousness by bright color patterns. Batesian mimicry evolves because mimics which tend to look like the model have a selective advantage.

If Batesian mimicry occurs in coral snakes, then venomous snakes must be the models, and must be mimicked by nonvenomous coral snakes. This can be determined empirically. Wallace (1867) proposed that for Batesian mimicry to occur, the following must be true:

> (1) That the imitative species occur in the same area and occupy the same station as the imitated.
>
> (2) That the imitators are always the more defenceless.
>
> (3) That the imitators are always less numerous in individuals.
>
> (4) That the imitators differ from the bulk of their allies.
>
> (5) That the imitation, however minute, is external and visible only, never extending to internal characters or to such as do not affect the external appearance.

-- Wallace, 1867, reprinted in Wickler, 1968, pp. 46-47

While Wallace's criteria need not always be met for Batesian mimicry to occur, (Wickler, 1968), they are often true and do provide some guidelines for investigating cases of mimicry. It is possible to determine whether the conditions are met. The authors of papers on coral snake mimicry have typically addressed at least some of these issues.

Mullerian mimicry is the resemblance of several unpalatable or noxious species to each other; it is a sort of "warning club" (Wickler, 1968). Typically, Mullerian mimics are fairly closely related. "... one does not speak of Mullerian mimicry when animals so different as the spotted salamander, the caterpillars of Cinnabar Moth and hornets all employ the same black-and-yellow warning coloration (Wickler, 1968, p. 78). Discussion of coral snake mimicry as a Mullerian complex is common (Dunn, 1954; Mertens, 1956; Wickler, 1968). For Mullerian mimicry to occur, it must be selectively advantageous for venomous coral snakes to look like each other. Batesian mimics commonly occur in Mullerian mimetic complexes and have even said to be "inextricably interwoven" (Owen, 1980).

Mertensian mimicry, as defined by Wickler (1968), occurs when highly noxious species mimic less noxious species. This has also become a popular explanation for coral snake mimicry. If Mertensian mimicry is responsible for coral snake mimicry, then the deadly venomous coral snakes must be the mimics, and the mildly venomous colubrids must be the models. Nonvenomous snakes can likewise mimic the mildly venomous snakes, and the mildly venomous snakes can form a Mullerian complex; thus, both Mullerian and Batesian mimicry can occur in a Mertensian complex (Wickler, 1968).

Coral Snake Mimicry in the Literature: Theoretical Treatments

According to Dunn (1954), "An almost complete acquaintance with the history, facts, and status of the coral snake mimic problem may be gained by the perusal of four papers; those of Cope 1860, Wallace 1867, Gadow 1911, and Sternfeld 1913" (p. 97). Cope (1860) first mentioned the coral snake mimicry "problem". Apparently, he suspected a typical Batesian mimicry complex. Dunn noted that Wallace (1867) considered there to be "a very remarkable and instructive case of mimicry." Gadow (1908) mentioned that coral snakes and their proposed mimics were often found in the same habitat, but in a later paper Gadow (1911) denied that coral snakes and their supposed mimics occurred close together. Gadow suggested that the coral pattern was concealing at dusk, when the snakes were presumably most active. He also noted that there were more presumed mimics than presumed models in Mexico. Sternfeld (1913, discussed in Dunn, 1954), pointed out that the coloration of supposed mimics in the range of the supposed models could not be attributed to coincidence; he further noted that only snakes which were within the range of size of the venomous coral snakes showed coral snake coloration.

Brattstrom (1955) discussed typical color patterns in snakes; he argued that bands serve a disruptive rather than a warning function, especially in snakes which were presumed to be active only at night. He noted that coral snakes, which comprised only 5.2% of the total number and 5.5 % of the total species in Dunn's sample are "relatively unimportant poisonous snake(s)". Brattstrom further argued that the extreme poisonousness of <u>Micruris</u> would be fatal for most predators, and that predators could not learn to avoid coral snakes. Therefore, there would be no selective advantage to nonvenomous snakes to mimic venomous coral snakes. Brattstrom concluded that the similarities in appearance of the various coral snakes were due not to mimicry, but to convergent evolution of a protective pattern.

In a paper which seemed to be primarily a rebuttal to Brattstrom, Hecht & Marien (1956) pointed out that the various colors of coral snakes are bright and adjacent areas strongly contrasted. Annulation is complete, extending across the ventral surface as well as the dorsal surface. They noted that sharply contrasting coloration has been shown in insects to be warning coloration, and that the selective advantage of similarity of dorsal and ventral colors may be important for pattern recognition by predators during manipulation of the prey. They concluded that the coral snake pattern is warning coloration.

Arguably the most thorough discussion of mimicry in coral snakes was that of Mertens (1966, discussed by Wickler, 1968). Wickler noted that Mertens, at first skeptical of coral snake mimicry, soon came to support it. After examining daily activity patterns, diet, size, and habitat, Mertens concluded that mimicry was the most likely explanation for coral snake coloration. He attempted to explain coral snake mimicry in terms of Batesian and Mullerian mimicry.

Mertens considered coral snake mimicry to be very old, perhaps older than sixty million years. He suggested that the mimicry may have evolved when coral snakes were less venomous. As the models became lethal, some of the original mimics became somewhat venomous. Thus, the models are not the highly venomous snakes, but the mildly venomous snakes, and both nonvenomous and highly venomous snakes are mimics. It was this explanation that caused Wickler to use the term "Mertensian mimicry" to explain coral snake coloration.

Greene & Pyburn (1973) made the following five points:

1. Their field experience and reports by other workers (Brattstrom, 1955; Gehlbach, 1970; Humphries & Driver; and Neill, 1959) suggest that coral coloration might serve a concealing function in the typical coral snake habitat.

2. Coral snakes bite when picked up, and it is therefore appropriate to consider that their coloration is aposematic.

3. Many predators of coral snakes can probably kill and eat them without being bitten; most bites of coral snakes are probably fatal to their predators. Mertensian mimicry assumes that learning occurs when predators have a distasteful experience with coral snakes. "Mertensian mimicry fails to explain the occurrence of harmless and highly venomous snakes in parts of Mexico and the southern United Snakes where there are no similarly patterned, mildly poisonous species" (p. 145).

4. "Selection on predator behavior, rather than learning, might be involved.... Formally stated, this explanation postulates an individually variable, genetically-based response of potential predators to brightly ringed snakes, so that some of them will tend to avoid such novel prey" (p. 146).

5. Predators may survive the bite of coral snakes, and thus learn to avoid snakes with the coral pattern. Observational learning may also occur.

Coral Snake Mimicry in the Literature: Empirical Evidence

Dunn (1949) reported on the relative abundance of snakes in a number of areas in Panama. His paper was the result of the study of a collection of over 11,000 specimens. The snakes had been collected for Dr. H.C. Clark. They were brought in by native collectors who received a fee of 25 cents for vipers and coral snakes, and 10 cents for other snakes. Dunn remarked that it was necessary to pay the differential because Dr. Clark suspected that 10 cents was not enough to induce the campesinos to bother with the more dangerous snakes. In Dr. Clark's collection, usually only the head and a short section of neck was turned in. Dunn remarked that he undoubtedly misclassified a substantial number of snakes. It is unfortunate that such a sacrifice of herpetological biomass was not undertaken more systematically; it is impossible, in retrospect, to know to what an extent the sample is representative of the true population. Dunn, however, concluded that the sample was fairly representative of the proportion of snakes in the wild.

Dunn (1954) used his 1949 data in the first of the "modern" papers about coral snake mimicry. He reported that 38% of the conspicuously ringed snakes in the sample were innocuous. Sixty-eight percent of the ringed snakes were definitely venomous. Dunn concluded that since venomous coral snakes were more numerous in his random sample than were non-venomous coral snakes, the conclusion that the non-venomous coral snakes were mimics of the venomous species was supported.

Hecht & Marien (1956) cited empirical evidence for coral snake mimicry. They noted that the milk snake of the northeastern United States, _Lampropeltis_ _doliata_ _triangulum_, where sympatric with the coral snake, _Micrurus_ _fulvius_, is annulated. The northern race of the milk snake lies outside the range of sympatry. Populations of the milk snake outside the range of _M._ _fulvius_ show variability in dorsal patterns and differences in dorsal and ventral patterns; the magnitude of those differences is positively correlated with the distance from the range of sympatry. They pointed out other such patterns with coral snake coloration within the range of sympatry with *Micrurus fulvius*, but with deviations outside the range of sympatry. This occurs with snakes of the genus *Sibynophis*, which presumably mimics *Micrurus fulvius*, and *Chionactis palorostris*, *C. occipitalis*, *C. klauberi*, and *C. annulata*, which are supposed mimics of *Micruroides*. Hecht & Marien suggested that if coral snake coloration is disruptive, there would be no reason for sympatric populations to be differently colored from populations outside the range of sympatry.

Hecht & Marien examined reports of frequency of occurrence of supposed models and mimics. They concluded, on the basis of reports by Carr (1940) (who unfortunately did not include data to back his assertions) that in a number of different biotopes in Florida *Micrurus* is more common or at least as common as the milk snake.

Mertens examined the frequency with which different species of snakes were brought into the Butantan Institut in Sao Paulo and discovered that if highly venomous coral snakes were considered to be models and both nonvenomous and mildly venomous snakes were considered to be mimics, then during four years the mimics outnumbered the models by a ration of about four-to-one (n = 277, 287, 323, 340). However, if the moderately poisonous species were considered to be models and both nonvenomous and highly venomous species considered to be mimics, then during the same four years the models are about three times more prevalent than the mimics. It is unclear from Wickler's discussion if Mertens rearranged his data in this way or if Wickler himself rearranged it.

Gehlbach (1972) suggested that the relative poisonousness of coral snakes was not important in coral snake mimicry, but that behavioral characteristics should be considered important. He indicated that the self-mimicry behavior of coral snakes might deter predators. Gehlbach therefore hypothesized that these snakes would show a lower percentage of injuries in the tail area than other snakes. He examined museum specimens to determine whether this was true. After examination of several hundred specimens, he found that the incidence of tail injuries in _Micrurus fulvius_ and _Micruroides eurxanthus_ was lower than for sympatric colubrid species. Tail injuries for color mimics were lower than for the population of non-mimics which lacked tail displays (this difference lacked statistical significance, however). Gehlbach interpreted this to mean that mimics might enjoy a selective advantage by looking like coral snakes.

Gehlbach constructed model "coral snakes" which he moved by means of strings. He found that juvenile coati mundis were frightened by the "self-mimicry" movements of the model coral snake, and that social facilitation seemed to occur; that is, when one coati ran away, the others did also. A control model which was painted olive green, was grabbed by coatis. Adult coatis were frightened by the self-mimicking model and avoided it after the first encounter. Gehlbach suggested that observational learning might result in predators learning to avoid coral snakes.

In two interesting studies Smith presented wooden dowels painted in various colors to inexperienced birds of two species, motmots (1975) and great kiskadees (1977). Motmots, a relative of the kingfishers, are found in Mexico and Costa Rica. Their primary food is lizards, and Smith speculated that small snakes might also be taken. Kiskadees inhabit semi-open habitats from Texas to Argentina. They feed upon small reptiles and *Micrurus*, and other species of coral snakes occur in various portions of the range. Smith speculated that in the wild both motmots and great kiskadees might be at danger from very venomous coral snakes. She removed hatchlings of both species from their nests; presumably these young birds were unlikely to have encountered coral snakes. Smith presented these birds with wooden dowels which were painted in coral snake colors in a ring pattern and coral snake colors in stripes; kiskadees were additionally tested with a white and green ringed pattern and a yellow and red ringed pattern. Before presenting these models, Smith determined that both species would not hesitate to peck at single-colored models of red, green, white, yellow, and black. The models which were painted to simulate coral snakes elicited alarm calls and avoidance reactions in both species. The red and yellow banded dowel caused less intense avoidance and fewer alarm calls in kiskadees. Smith considered her results to be a strong indication of innate recognition of coral snake patterns in these two species.

Can Learning Account for Coral Snake Mimicry?

The extent to which learning figures into the evolution of and maintenance of coral snake mimicry is unclear. Although Gehlbach (1972) has suggested that observational learning may be a causal factor in coral snake mimicry, there is no direct evidence of predators learning to avoid coral colored snakes. Whether elapid coral snakes are so deadly that predators do not survive encounters with them has been a controversial point. The case is not so clear as in insect mimicry, where a number of studies have demonstrated that predators learn to avoid noxious insects which are mimicked by other insects (Boyden, 1976; Brower, 1960; Coppinger, 1970; Owen, 1980; Wickler, 1968). This presumably results in differential selection upon species which are potential mimics, favoring those individuals which look most like the models.

Most predators of very venomous coral snakes, especially avian predators, can presumably escape being bitten because of their method of capturing these snakes (Gehlbach, 1972; Greene & Pyburn, 1973; Smith, 1969;). Bitten animals are at grave risk. The venom of elapid coral snakes is very potent. Wickler (1968) noted that a mouse bitten by _Micrurus_ _corallinus_ or _M_. _fulvius_ will drop dead on the spot. A major problem many workers have had in accepting that the elapid coral snakes are models is this extreme venomousness. Wickler (1968) and others have suggested that predators could learn nothing by an encounter with a coral snake since they would either be bitten, and thus dead, or unbitten and unaffected. This seems to be a simplistic assumption. It is likely that predators can sometimes survive the bite of the very venomous coral snakes. Poisoning is an adaptation for obtaining food (Porter, 1972); it is very effective for this, for large amounts of poison relative to the size of the prey are typically injected. Poisonous snakes do bite, and some are more likely to bite than others (Porter, 1972), but this may be due more to the immediate effects of the bite and its associated behavior than to the relatively long-term effects of poison. It does seem unlikely that envenomation would evolve as an antipredator mechanism; however, if there is a differential reproduction rate of snakes which envenomate predators and those which do not, then it would be possible for a poison delivery system to evolve as a deterrent for predators. However, since poison would undoubtedly increase the efficiency of the snake itself as a predator, it would be difficult or impossible to determine the differential selective advantages of each.

The poison delivery system of the elapid coral snakes is not as specialized as that of the pit vipers (Porter, 1972), and may be less effective in the delivery of poison. Furthermore, the relatively small jaws of the very venomous coral snakes make it very difficult for these snakes, especially smaller specimens, to pierce the skin of larger animals (Conant, 1975). Feathers and fur are probably effective protection from the bite of many of these snakes. Poisoning of a predator, although it may prove fatal, would seem to be of little advantage to an individual poisonous snake, for it would likely be dead and perhaps eaten before the predator would be disabled or killed. It might be of advantage to the snake to bite predators, but to inject less poison or perhaps no poison at all; there is some evidence that at least some venomous snakes can control the amount of venom injected.

Larger predators would tend to be less affected than small ones. Neill (1957) collected cases of human snakebite by coral snakes. Of 20 reported cases, many involving children, 16 individuals recovered and 4 individuals died. In some of the cases, although the fangs penetrated the skin, there were no ill effects or only mild effects noted; this suggests that variable amounts of venom were introduced into these individuals. While it is possible that the poison of the snakes may have been temporarily exhausted, it seems more likely that less than a maximal amount of venom was injected. Although many of the bitten humans received intensive medical care, others did not, and by extrapolation it seems likely that a fair proportion of bitten predators may survive the bite of coral snakes. It has been suggested that only slight differences in fitness rates are sufficient for a trait to spread through a population (Barash, 1982).

Bites of less venomous colubrid coral snakes probably result in fewer fatalities among predators, and hence avoidance learning may be more likely to occur. It is likely that this is a mechanism which is at least partly responsible for maintaining mimicry in coral snakes at the present time, but which probably does not account for its origin. Wickler (1968) noted that there has a tendency toward increasing toxicity of venom among the coral snakes, and Mertens (1956) concluded that the coral coloration in elapid snakes is at least 60 million years old. It would be of interest to know definitely whether the coral pattern of these snakes evolved first among the elapids or among the colubrids; unfortunately, the fossil record is unlikely to preserve this information. However, the coral pattern of colubrids tends to occur only in areas in which they are sympatric with very venomous elapids (Emsley, 1966). If coral snake coloration occurred first in these species, and if the very venomous coral snakes were mimicking the less venomous species, then the colubrids should show coral snake coloration throughout their range, and the elapids only where they are sympatric with the colubrids; the actual case is just the opposite (Hecht & Marien, 1956).

Erratic behavior or the self-mimicry discussed by Gehlbach (1972) might be a more effective antipredator behavior than poisoning. Such behavior has been demonstrated to deter ophidian predators (Gehlbach, 1970) and coati mundis (Gehlbach, 1972), and Coppinger (1970) has demonstrated that birds tend to avoid brightly colored novel food items. Avoidance of coral snakes by predators which have been frightened by "self-mimicry" could result in a selective advantage for mimics.

Observational learning (called by Gehlbach empathic learning or social facilitation) could account for coral snake mimicry, but only if snakebite is fairly frequent, and only by social predators. Observational learning would be unlikely to occur in solitary predators. The "self-mimicry" of coral snakes seems to be a definite anti-predator response and the ways in which it interacts with coral snake coloration certainly warrants further investigation.

If predators are unable to survive the bite of a coral snake, then experiental learning could not account for avoidance of coral snakes by predators, and thus a selective advantage for coral snake mimics. In cases of fatal bite, observational learning could account for a learned avoidance of coral snakes, but only in social predators. Experiental learning as the result of self-mimicry might result in continuing avoidance of coral snakes and their mimics; it remains to be seen whether this occurs. Various types of learning by predators, while a plausible mechanism for the evolution of and maintenance of coral snake mimicry, has not been demonstrated.

Can Natural Selection Account for Coral Snake Mimicry?

> ... the process of selection cannot be regarded as a metaphysical force; selection is a consequence of a quite specific causal system and selective effects are passive and automatic.
>
> -- Wickler, 1968, p. 39

Although natural selection has been suggested as a mechanism for mimicry in snakes (Gans, 1961; Greene & Pyburn, 1973), this has not been systematically investigated in coral snakes, or for that matter, in any species. To demonstrate an innate response to the coral pattern in snakes, assumptions must be made that (1) there will be individual variation in this response among predators; and (2) predators most likely to encounter coral snakes will have reduced fitness (Greene & Pyburn, 1973).

> If these conditions are met, selection would favor individual predators which avoid the brightly marked venomous snakes. This could in turn promote the evolution of a mimetic complex involving one or more harmless species. Verification of this hypothesis would require demonstration of genetically influenced avoidance reactions by relevant predators-- those that will attack snakes but that can be killed or seriously injured by the bite of a venomous coral snake.
>
> -- p. 146

It is unclear whether differential selection of predators which avoid coral snakes should lead to passive or active avoidance of coral snakes. Rubinoff & Kropach (1970) demonstrated that predators from the Pacific Ocean did not attack the Pacific sea snake *Pelamis platurus*.

Typically, predators showed no interest in these snakes, or, if they swallowed them, spat them out and thereafter ignored them. Atlantic predators did attack these snakes, and were sometimes wounded in the process. Smith's (1975, 1977) demonstrations that naive birds show alarm calls and avoidance responses to coral snake patterns suggest that these potential predators actively avoid coral snake patterns. Smith's findings provide strong evidence that natural selection is a mechanism in the evolution of mimetic systems. In coral snakes natural selection may, indeed, be the primary mechanism. This is of great theoretical importance and further investigation is indicated. A replication of Smith's studies with other coral snake predators is especially indicated; this should be done in another laboratory to rule out procedural and artifactual effects. Because empirical evidence indicates that very venomous coral snakes are the models in the coral snake mimetic complex, further investigation should center on the effects of these models upon predators. The relationship between the defensive displays of very venomous coral snakes, their coloration, and the effects on predators warrants particular investigation.

Sociobiology and Coral Snake Coloration

It is surprising that the mimetic system of the New World coral snakes has not attracted the attention of sociobiologists. The basic descriptive groundwork, ecological and behavioral studies, and a great deal of theorizing, as well as several empirical studies of the reactions of potential predators to coral snakes have been done by herpetologists. What remains to be done is to determine the relative importance of natural selection and various types of learning to the coral snake mimetic system. A sociobiological explanation of coral snake mimicry might be as follows:

> At some time in the past, venomous New World serpents of the family Elapidae evolved an aposematic (warning) coloration. Predators which approached these snakes were sometimes bitten, and as a result of the bite had reduced fitness; that is, they died, or else had fewer progeny as a result of sickness from the bite. Genes which coded for avoidance of (a) brightly colored prey; (b) prey with unusual coloration; or (c) specific coral snake patterning were thereby reduced in frequency in the gene pool of the predators. Selective pressures resulted in a common aposematic pattern, the coral pattern, in many

> different elapid species; that is, very venomous elapid snakes which tended to join a "warning club" had higher fitness than did the snakes which did not join the "warning club". Because colubrid snakes which resembled very venomous elapids of this "warning club" were avoided by predators, selective pressures were less on mimics, and a number of species evolved coral snake coloration. Outside the range of the very venomous snakes, selective pressures did not favor coral snake coloration, and a cryptic (blotched) pattern was often favored instead.

In this scenario, learning by individual predators plays but a minor role in the evolution of coral snake mimicry. The entire mimetic complex evolved and is maintained by differential inclusive fitness of predators which avoid coral snakes and predators which do not avoid coral snakes. The very venomous coral snakes are the models, and both the mildly venomous and nonvenomous species are the mimics.

It is possible to test this sociobiological hypothesis. In this instance, the following hypotheses might be made:

> (1) Naive predators which are sympatric with coral snakes will show strong avoidance responses to coral snake patterns. Other patterns will elicit less extreme reactions. Predators will show stronger responses to coral snake patterns which occur in their habitats than to patterns which occur only elsewhere. Predators from areas with no coral snakes will not show this avoidance.
>
> (2) Models (colubrids) will vary with mimics (elapids). Colubrid coral snakes which are sympatric with differently colored isolated populations of elapid coral snakes will look like the very venomous coral snakes where they are sympatric, but not elsewhere; that is, one species of model may mimic two species of models.

Evidence for both points 1 (Smith, 1975, 1977) and 2 (Greene, personal communication) is already in existence. Confirmation would serve to damage the notion of Mertensian mimicry, which has been suggested for other mimetic systems in snakes (Gans & Latifi, 1973; Kroon, 1975).

Discussion

Very venomous coral snakes are relatively rare in their habitat and do not seem to make up the bulk of the diet of any predator. They are not particularly prone to bite and may have trouble in biting some predators. Their bite is very toxic and probably results in a high mortality rate among bitten predators. All of these factors suggest that operant learning would seem not to be the mechanism whereby coral snakes, both models and mimics, enjoy protection from their coloration. Although it has been shown that long latencies between environmental events and their consequences can result in learning, as demonstrated by the research of Garcia & Koelling (1966) and others, such learning seems to be an adaptive mechanism associated with ingestion of food and would not occur when predators do not consume very venomous coral snakes after being bitten. Even if social learning can function in predator avoidance, it seems unlikely that conspecifics would associate fatality with an encounter with prey which occurred some minutes or hours before. For these reasons, learning as a result of being bitten by very venomous coral snakes does not seem to be the mechanism whereby coral snake mimicry evolved or is maintained.

There is considerable evidence that bizarre behavior and unusual coloration of prey can deter predators. Perhaps the defensive posture of the very venomous coral snakes is the mechanism whereby coral snake coloration provides a selective advantage. It should be possible to simulate this behavior in the laboratory, as Gehlbach (1972) did in semi-natural settings.

An alternative hypothesis, and one which has apparently not been explored, is that very venomous coral snakes have a noxious taste. This could be easily verified if some brave soul tasted coral snakes. This is unlikely, for coral snakes do not seem to feed mainly or exclusively upon noxious species, and other snakes seem to eat coral snakes avidly.

If mechanisms for coral snake mimicry which involve learning are eliminated, then coral snake mimicry must have a genetic basis. If this is true, then mimicry in coral snakes is maintained by a different mechanism than is Batesian mimicry in other species which have been demonstrated to depend upon aversion learning. If coral snake mimicry could be demonstrated to depend upon selective elimination of genes in a population of predators, then coral snake mimicry would indeed rate a term of its own.

Conclusions

Existing data indicate that very venomous elapid coral snakes are mimicked by both nonvenomous and mildly venomous coral snakes. Natural selection operating upon predators is the mechanism most likely responsible for the evolution of mimicry in coral snakes. Mertensian mimicry and learning may function in maintenance of this mimetic system.

Summary

Examination of contributions to the literature of coral snake mimicry suggests that coral-colored snakes of the family Elapidae are warningly colored, and are mimicked by nonvenomous and mildly venomous colubrid snakes. Natural selection operating upon predators may be the primary causal mechanism for this unusual mimetic complex. Learning and Mertensian mimicry does not appear to be responsible for the evolution of this complex, although they may operate in its maintenance. The importance of coral snake coloration for biological theory is considerable, and further investigation, especially replication of the findings of Smith (1975, 1977) is indicated.

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