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DIFFERENTIAL AVOIDANCE OF CORAL SNAKE BANDED PATTERNS BY FREE-RANGING AVIAN PREDATORS IN COSTA RICA

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Abstract.—Empirical studies of mimicry have rarely been conducted under natural conditions. Field investigations of some lepidopteran systems have provided a bridge between experiments examining artificial situations and the mimicry process in nature, but these systems do not include all types of mimicry. The presence of dangerous or deadly models is thought to alter the usual rules for mimicry complexes. In particular, a deadly model is expected to protect a wide variety of mimics. Avoidance of different types of mimics should vary according to how closely they resemble the model. Coral snake mimicry complexes in the neotropics may provide natural systems in which these ideas can be examined, but there is no direct evidence that the patterns of venomous coral snakes or potential mimics are avoided in the wild. Plasticine replicas of snakes were used to assess the frequency of avian predation attempts as a function of color pattern. Avian predators left identifiable marks on the replicas, the position of which indicated that replicas were perceived as potentially dangerous prey items by birds. The number of attacks on unmarked brown replicas was greater than that on tricolor coral snake banded replicas. This result was true whether replicas were placed on natural or plain white backgrounds, suggesting that coral snake banded patterns function aposematically. In a separate experiment, replicas representing all six patterns of proposed coral mimics at the study site were attacked less often than unmarked brown replicas. Within these six banded patterns, some were attacked significantly more often than others. This study provides direct field evidence that coral snake banded patterns are avoided by free-ranging avian predators and supports theoretical predictions about mimicry systems involving deadly models.

Key words.—Adaptive coloration, antipredator mechanisms, aposematism, elapid snakes, mimicry, vertebrates.

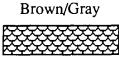


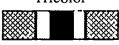



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
Encounters between predator and prey are rarely observed in nature. For this reason, most proposed mimicry systems have been evaluated using indirect evidence, typically parallel geographic variation in model and mimic species (Pough, 1988*a*). Only recently have experimental tests of mimicry been conducted with wild predators under natural conditions and, with one exception (Brodie and Brodie, 1980), these are restricted to a few invertebrate or artificial model-mimic systems (reviewed in Waldbauer, 1988). Researchers have had to rely almost exclusively on data from artificial systems (i.e., using models and mimics that do not represent real organisms, such as colored pastry baits) and controlled experiments (e.g., with caged predators) for validation of theoretical predictions, causing some authors to question the applicability of existing theory to mimicry systems in the wild (Waldbauer, 1988).

Two general predictions that have remained untested in natural mimicry systems are that extremely repulsive or dan-

gerous models should protect a range of imprecise mimics (Duncan and Sheppard, 1965; Goodale and Sneddon, 1977) and that some protected patterns are more effective mimics than others (Sexton, 1960; Alcock, 1970; Morrell and Turner, 1970; Pilecki and O'Donald, 1971; Shideler, 1973). Coral snake mimicry complexes in the neotropics may have features that would allow tests of these hypotheses in the wild, but the identity of the models and range of protected mimics in these systems are still unclear. In fact, there is no direct evidence that coral snake patterns function aposematically or are avoided by visual predators in the wild (reviewed in Pough, 1988*a*).

Pough (1988*a*, 1988*b*) suggested that mimicry of venomous snakes may permit imprecise resemblance by mimics because of the severe consequences of mistakenly attacking a model (Brugger, 1989). The primary evidence in support of this theory is the variety of snakes that have been proposed to mimic the red, yellow, and black banded venomous coral snakes of the genus

Color Pattern	Venom	Species
	+	<i>Conophanes fissidens</i>
	+	<i>Rhadinea sp</i>
	-	<i>Geophis hoffmanni</i>
	-	<i>Chironius grandisquamis</i>
	-	<i>Mastigodryas melanolomus</i>
	+	<i>Clelia clelia</i> (juv.)
	-	<i>Ninia sebae</i>
	-	<i>Lampropeltis triangulum</i>
	++	<i>Micrurus nigrocinctus</i>
	++	<i>M. alleni</i>
	+	<i>Erythrolamprus mimus</i>
	-	<i>Scaphodotophus venustissimus</i>
	++	<i>Micrurus multifasciatus</i> (common morph)
	+	<i>Oxyrhopus petola</i>
	+	<i>Liophis epinephalus</i> (only during display)
	++	<i>Micrurus multifasciatus</i> (rare morph)
	+	<i>Urotheca euryzonus</i> (rare morph)
	+	<i>Urotheca euryzonus</i> (common morph)

 BROWN
  WHITE
  BLACK
  RED
  YELLOW

++ venomous elapid + rear-fanged colubrid - nonvenomous colubrid

FIG. 1. Snake species with various banded and unmarked gray or brown patterns occurring at La Selva Biological Station, Costa Rica. The venom delivery system of each species is noted. Legend below explains color pattern depiction and venom delivery notation.

Micrurus (e.g., Pough, 1988a, 1988b; Campbell and Lamar, 1989). These snakes range from very precise mimics with geographic variation in color pattern that closely parallels that of sympatric coral snakes (Greene and McDiarmid, 1981) to species with only small portions of the body bearing black and red or yellow bands (Greene, 1975; Henderson and Hoeffers, 1977; Henderson, 1984; Pough, 1988a, 1988b). Experiments with caged naive birds suggest that the red, yellow, and black banded pattern of true coral snakes, and at least two other similar patterns not found on any real snake species, are innately avoided by potential predators (Smith, 1975, 1977). Studies of artificial mimicry systems indicate that birds trained with highly noxious models avoid

mimics that are less similar than birds trained with milder models (Duncan and Sheppard, 1965; Goodale and Sneddon, 1977). However, it is not known which banded patterns of snakes are actually avoided by free-ranging predators, so conclusions based on the variety of presumed mimics are unfounded.

In the Atlantic lowlands of Costa Rica, three species of venomous elapid coral snakes are sympatric with several non- or mildly venomous (rear-fanged) colubrid snakes with bright banded patterns (Fig. 1). Two of the coral snakes have tricolor banded patterns (red-yellow-black-yellow-red; the "tricolor monad" of Savage and Slowinski, 1992), whereas the third has a red and black bicolor banded pattern, but also occurs in a rare white and black morph (Villa, 1972; Fig. 1). The sympatric snake species with banded patterns that have been proposed as mimics can be placed into six pattern categories: the three above, plus reverse tricolor (red-black-yellow-black-red; the "tricolor dyad" of Savage and Slowinski, 1992), collared (black and yellow bands on the neck only with a red body), and bicolor banded with a stripe (white and black bands with a red dorsal stripe apparent only on the white bands) patterns (Fig. 1). Several non- or mildly venomous sympatric snakes are uniformly brown or gray dorsally, or possess very faint lateral stripes (Fig. 1). None of the venomous elapid or viperid snakes has a color pattern of this sort. To assess the relative frequencies of attacks by birds on these different patterns, and to learn whether the tricolor coral snake banded pattern functions aposematically, I exposed plasticine replicas with these patterns to free-ranging avian predators. Beak imprints left by birds on the replicas allowed me to determine which color patterns were avoided under natural conditions.

MATERIALS AND METHODS

Replica Construction and Transect Placement

Identical replica-production techniques were used in each of the two experiments. Snake replicas were constructed using pre-colored, nontoxic plasticine (Sculpey-III modeling compound) threaded onto a wire



FIG. 2. Tricolor coral and unmarked brown replicas placed on (A) plain white paper and (B) a natural background in the aposematism experiment. Replicas were placed together for illustrative purposes only (see text for description of actual placement).

frame. The use of soft replicas is a particularly powerful method for estimating infrequent predation attempts because large samples may be used and replicas “remember” disturbances through impressions in their surfaces. It is therefore possible to distinguish attacks by birds from other disturbances (cf. Madsen, 1987).

Replicas were constructed by threading cylindrical slices of different colors onto an S-shaped wire. This method provided a replica 1 cm in diameter and 16 cm in length; approximately the diameter of an adult *Micrurus nigrocinctus*, the most common tricolor coral snake in the area of study (other potential model and mimic species have comparable diameters). For all banded replicas, the banding pattern was reproduced as it would appear on the anterior portion of the snake (so that each replica had a “head” pattern on at least one end). Models were anchored to the ground by means of a 3 cm length of wire protruding from each end of the model.

To assess avian predation under natural conditions, replicas were placed at 10 m intervals along transects through primary and secondary forest along the trail system at La Selva Biological Station, Costa Rica. Replicas were placed on the forest floor 0.5 m from the edge of the trail at each interval. The order of replica types was randomized separately for each transect. After 48 to 72 hr (see below), replicas were picked up, reshaped, and relocated to a new transect at

least 1 km away. Because replicas were relocated, attacks during different transect periods were considered statistically independent.

Experiment 1: Aposematism

In March 1989, tricolor coral snake banded and unmarked brown replicas were placed on two different backgrounds (Fig. 2) to determine if free-ranging birds attacked an unmarked brown pattern more often than a coral banding pattern, and if so, whether this was because the coral banding pattern was actively avoided or simply not noticed (i.e., cryptic). Fifty-one models of each type were constructed and placed on natural backgrounds (the forest floor) for two 48 hr transect periods (Fig. 2). This procedure was then repeated by placing each model on a 12.5×20 cm piece of white paper to remove any possible cryptic effects of the color patterns (Fig. 2). Each of the four transects (a total of 408 replica events) was conducted in a nonoverlapping area of the forest.

Experiment 2: Relative Mimetic Advantage

In February–March 1990, replicas were constructed representing all six of the banded color patterns found on snakes present at La Selva, plus the unmarked brown control (Fig. 1). Band widths and sequences were determined through field observation and inspection of museum specimens at the

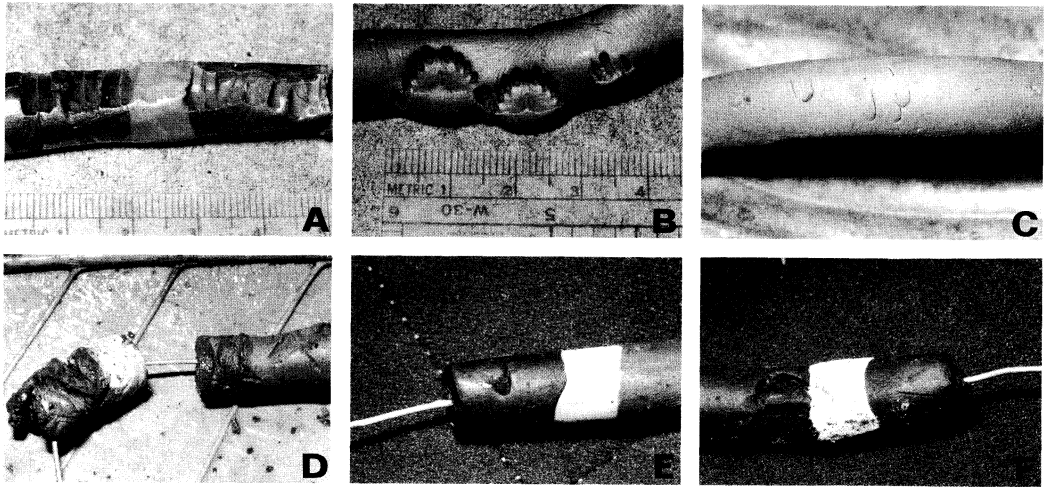


FIG. 3. Imprints left by attacks on snake replicas in the field. (A) Incisor marks from a large rodent (probably agouti); (B) opossum (*Didelphidae*) toothmarks; (C and E) U-shaped bill marks from birds; (D) a replica torn apart and displaced by a bird; (F) serrated bill marks from a motmot attack.

University of Texas at Arlington Collection of Vertebrates. Fifty replicas of each pattern (350 total) were placed on natural backgrounds for 72 hr periods. A total of six transects were conducted (a total of 2,100 replica events), covering all available trail space at La Selva without repeating any sections. A full day was needed to reshape the replicas, so sequential transects started five days after the previous one.

Scoring and Testing

The approximate size and shape of each mark was noted, as well as the position of the mark on the model. Replicas often had more than one mark (of the same type) on their surfaces. In these cases, only one disturbance was scored because of the possibility that these were multiple marks from the same event. In the second experiment, five models (one model in each of five transects) were not found during recollection. These were conservatively scored as undisturbed because of the chance that I simply could not find them again. Spatial effects were investigated by reanalyzing the avian attack data after removing all instances where consecutive strings of every, or every other replica were attacked. Series of consecutive attacks might be due to an individual bird moving along the transect. This analysis was included to determine if such behavior affected the results.

All analyses were performed using *G*-tests. Unplanned tests of homogeneity were used to identify sets of replicas that experienced different frequencies of disturbance in the relative mimetic advantage experiment (Sokal and Rohlf, 1981, pp. 728–729). An experimentwise level of significance was taken at $P < 0.05$ in all cases where unplanned tests of homogeneity were performed.

RESULTS

Marks Found on Replicas

In both experiments, bird attacks on the models could easily be recognized as a pair of V- or U-shaped marks on opposite sides of a replica or as a closely spaced, matched pair of stabs on the dorsal surface of the replica (Fig. 3C–F). On some of the V- and U-shaped marks, an imprint made by a ridge in the upper mandible was apparent (Fig. 3C). Most replicas with beak imprints in them bore multiple marks, normally clustered within a 2 to 3 cm section of the replica (Fig. 3C and D). In some instances, replicas had one or both ends ripped off or had been pulled from the ground and displaced up to 1 m away (Fig. 3D). The shapes and nature of these marks, together with the nonrandomness of their distribution with respect to pattern of and position on the replicas (see below), indicate that events not specifically directed at the replicas (e.g., falling

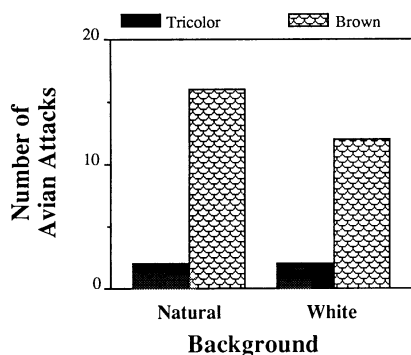


FIG. 4. The number of avian attacks on tricolor coral and unmarked brown replicas placed against natural or plain white backgrounds.

leaves or branches) could not account for such marks.

Potential avian predators seen in the area of the transects included several species of motmots (Momotidae), puffbirds (Bucconidae), kiskadees (Tyrannidae), cuckoos (Cuculidae), and various antbirds (Formicariidae) and raptors. A variety of shapes and sizes of avian marks on replicas was observed, but specific marks were not assignable to species because of the similarity of bill shapes among bird taxa. However, a few of the marks could be attributed to motmots because of the size and distinctive serrated edges (Fig. 3F).

Other forms of identifiable disturbance included small rodent, agouti (Fig. 3A), and didelphid (Fig. 3B) toothmarks, mandible marks from ants (including, but not limited to *Atta cephalotes*), peccary hoofprints (identifiable from disturbance in the adjacent area), and human bootprints. These and other unidentifiable marks were categorized as "nonavian disturbance" because they came from sources unlikely to be visually oriented snake predators.

Experiment 1: Aposematism

In the first experiment, coral snake banded replicas received fewer attacks by birds than did unmarked brown replicas (Fig. 4). This result was true when replicas were placed either on natural backgrounds ($G = 13.46$, $df = 1$, $P < 0.0001$) or on white paper ($G = 8.46$, $df = 1$, $P < 0.005$; Fig. 4). The frequency of avian attacks on all models did not differ between the two backgrounds ($G = 0.54$, $df = 1$, NS).

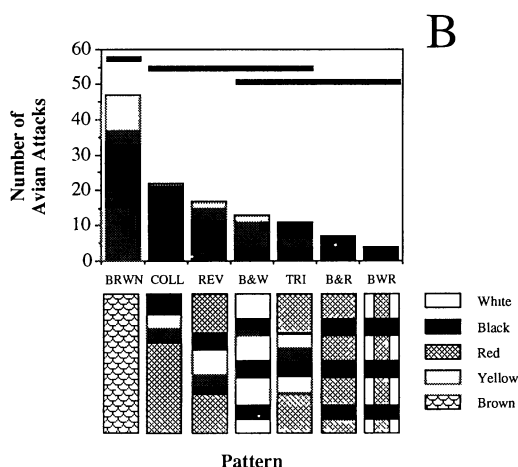
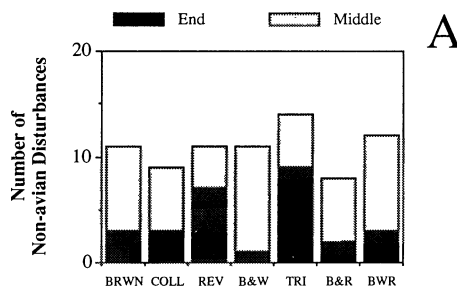


FIG. 5. The number of (A) nonavian disturbances and (B) avian attacks on each of the seven replica types in the relative mimetic advantage experiment. Solid bars indicate the number of attacks on the middle of a replica, stippled bars indicate the number of attacks on the distal portions of a replica. Solid lines above the bars in (B) indicate groups that differ significantly from each other in the total number of avian attacks. The patterns used appear below the graphs: **BRWN** = unmarked brown, **COLL** = collared, **REV** = reverse tricolor, **B&W** = black and white, **TRI** = tricolor, **B&R** = black and red, and **BWR** = black and white banded with red dorsal stripe.

Experiment 2: Relative Mimetic Advantage

Position. — End attacks were taken as those to the distal 3 cm of either end of any replica. Comparing the frequency of replicas with attacks on the ends to the proportion of a replica comprised of this region (37.5%) showed that avian predators directed attacks disproportionately towards an end ($G_p = 134.64$, $df = 6$, $P < 0.0001$; Fig. 5B). The distribution of nonavian disturbances was random with respect to position on the replica ($G = 0.01$, $df = 1$, NS; all patterns pooled because of small expected cells; Fig. 5A).

Pattern Type. — When all disturbances not

assignable to birds (including those made by rodents, ants, human boots, or unidentifiable sources) were combined, no significant differences in frequency of attack among any of the pattern types were observed ($G_H = 2.11$, $df = 6$, NS; Fig. 5A).

The number of replicas attacked by avian predators differed significantly among pattern types ($G_H = 66.5$, $df = 6$, $P < 0.0001$; Fig. 5B). Unmarked brown replicas were attacked significantly more often than all other patterns ($G_H = 12.7$, $df = 6$, $P < 0.05$). Among the six remaining banded patterns, two overlapping significance groups were detected (Fig. 5B). The white and black with a red stripe (1.3% attacked) and red and black (2.3% attacked) replicas experienced significantly fewer avian attacks than both the collared (7.3% attacked) and the reverse tricolor (5.3% attacked) replicas.

Spatial Effects.—The qualitative results were unchanged when consecutive attacks were removed from the analysis. Thirteen consecutive attacks (five reverse tricolor, four black and white, three tricolor, and one red and black) occurred in four separate series. Significance levels remained the same, but values of the G -statistics were slightly larger.

Order Effects.—The total number of avian attacks on all replicas in a transect did not change over the course of the study. A Spearman rank correlation detected no association between the number of avian attacks and date ($r_s = 0.086$, NS).

DISCUSSION

Avian Predation Attempts

The nature and position of the beak imprints suggest that birds perceive and handle the plasticine replicas as reptilian prey rather than nonprey items. Virtually all of the replicas with beak imprints were marked within 3 cm of an end. In many cases, the end was actually severed from the rest of the replica. Nonavian disturbances were distributed randomly with respect to position on the replicas, indicating that there was no bias towards contact with an end due to placement or construction of the replicas. Smith (1973, 1976) has shown that two avian predator species of reptiles have a congenital tendency to attack potential

prey behind the head. If no head, as represented by eyes or a constriction in the shape, is present, naive loggerhead shrikes and motmots attack an end. This behavior is viewed as an adaptation for handling dangerous prey such as snakes, that can inflict injury with their teeth (or fangs) if the head is not immobilized immediately (Smith, 1973, 1976).

Experience with the plasticine replicas did not appear to alter the behavior of avian predators. Over the five week period of the relative mimetic advantage experiment, avian attack frequencies did not decrease. If birds learned that the replicas were inedible and were able to recognize them as such, one would expect to see a gradual decrease in the total number of attacks per transect. The absence of this trend suggests that birds were unable to distinguish replicas from potential food items, or that different individual birds were responsible for the attacks in different transects. Within a transect, spatially clustered attacks might have resulted from a single predator. A reanalysis of the relative mimetic advantage data after all clusters of attacks were removed did not alter the results. The predatory behavior of a few individuals apparently was not responsible for the outcome of the experiment.

Because plasticine replicas possess no behavioral repertoire, the avian attack frequencies estimated by this methodology may not be accurate estimates of actual attack frequencies on snakes in nature. Antipredator behaviors of living snakes should cause some interactions with birds to end without a successful attack; such instances would result in beak imprints on a behaviorless replica. Conversely, some predators may use movement to detect snakes, and therefore would not attack a motionless replica. However, all replicas have the same behavioral potential to attract or repel predators, so these considerations should not affect the relative number of attacks on the various replicas. The plasticine replica technique controls for differences in antipredator behavior that exist among snake species, thereby allowing the assessment of relative risk of attack as a function of color pattern in a specific behavioral context (a motionless S-shaped posture).

Aposematism

Coral snake banded replicas significantly fewer attacks by birds than did unmarked brown replicas when placed on natural backgrounds, suggesting that snakes with coral snake banded patterns are subject to less predation than those without such patterns. Although this establishes a selective advantage to a coral snake banded pattern under field conditions, it does not elucidate the function of the pattern. A difference in the frequency of attacks on the two patterns may result from an aposematic effect, whereby predators actively avoid the coral banding pattern, or from a cryptic effect, whereby predators do not notice the coral snake banded pattern as readily as the unmarked brown pattern.

The differences in attack frequencies on the tricolor coral and unmarked brown models persisted on the plain white background. This indicates that the lower number of attacks on the tricolor coral pattern is due to avoidance of, rather than a cryptic effect of, this pattern in the context of a natural background. Discrepancies in attack frequencies on unmarked brown and banded plasticine replicas thus represent differential preference or avoidance of these patterns by avian predators. While other lines of evidence support the view that motionless coral snake banded patterns are aposematic (reviewed in Greene and McDiarmid, 1981; Pough, 1988*a*, 1988*b*), it is still plausible that such patterns are also cryptic in some situations. Behavioral components of crypsis, such as flicker-fusion effects and evasive flight (Brattstrom, 1955; Jackson et al., 1976; Pough, 1976; Brodie, 1989), may sometimes operate to make banded patterns cryptic in live snakes.

Relative Mimetic Advantage

All replicas with banded patterns were attacked less often by avian predators than were those with an unmarked brown pattern, but some banded patterns suffered more avian attacks than others. The results of the aposematism experiment indicate that the discrepancies in attack frequency between the banded and unmarked brown patterns in the relative mimetic advantage experiment are due to avoidance of banded patterns by visual predators.

All of the replicas can be considered mimics of real snake species. The replicas had no "defenses" other than color pattern, and it is clear that birds did not learn to recognize them as unprofitable prey items because there was no decrease in the overall attack frequency over the course of this study. Any avoidance of particular replica patterns should therefore be due to their resemblance to actual snakes. The avoidance of banded replicas establishes a mimetic advantage of brightly banded patterns on elongate objects in nature.

Which species and patterns serve as models and mimics in this complex is not clear. This experiment alone can not rule out the possibility that all banded snakes are avoided because of their own qualities as potentially dangerous or unprofitable prey. However, both brown and banded patterns are found on rear-fanged colubrids at La Selva, and one of the banded patterns (reverse tricolor) is only found on a nonvenomous snake. It is improbable that snakes with banded patterns are avoided because each species is more repellent than unmarked brown snakes.

The most likely scenario is that banded colubrids are protected through Batesian and perhaps Müllerian (in the case of rear-fanged species) mimicry of elapid coral snakes. Previous studies indicate that some avian predators have evolved avoidance of true coral snake banded patterns, but that they also avoid similar patterns not found on real snakes (Smith, 1975, 1977). Congenital avoidance probably evolved as a result of the consequences of attacking deadly prey (Greene and McDiarmid, 1981; Brugger, 1989). Both elapid coral snakes and some of the rear-fanged colubrids may have the potential to exert this kind of selection. Because the same color patterns are shared by many snake species at most localities, dissection of the precise pattern of Müllerian and Batesian relationships among taxa is probably impossible.

It has also been proposed that noxious millipedes may serve as models for mimicry complexes involving banded reptiles (Vitt, 1992). I know of no millipedes with banded patterns at the study site, but strikingly banded millipedes are present and abundant in other parts of the neotropics and

may be important components of other coral snake mimicry systems.

Mimicry of Venomous Reptiles

The results of this study support some of the predictions about differences between classical mimicry systems and those involving dangerous models, especially venomous reptiles (Pough, 1988*b*). Encounters with venomous snakes can have severe consequences, including death, for predators (Greene and McDiarmid, 1981; Pough, 1988*a*, 1988*b*; Brugger, 1989). For this reason, it is thought that predators should evolve innate avoidance of dangerous prey and that avoidance should be generalized to a wide range of imprecise mimics. For mimicry systems involving coral snakes, Smith's (1975, 1977) work with captive naive birds supports the first prediction. The evidence for the second prediction is limited to the existence of a variety of red, yellow, white, and black banded patterns on snakes throughout Latin America (Pough, 1988*a*, 1988*b*; Campbell and Lamar, 1989; Savage and Slowinski, 1992). None of these patterns, including those of the presumed models, true coral snakes, was known to be avoided by free-ranging predators in nature. The data presented here support the general opinion among herpetologists that brightly banded neotropical snakes are mimics of elapid coral snakes (e.g., Savage and Slowinski, 1992), and strengthens Pough's (1988*b*) contention that this variety of banded patterns is evidence that deadly models protect a wide range of imprecise mimics.

In systems with a variety of mimics, the relative mimetic advantage of each morph is predicted to decrease as similarity to the model decreases. Experimental work with artificial mimicry systems and predators supports this view (Sexton, 1960; Alcock, 1970; Morrell and Turner, 1970; Pilecki and O'Donald, 1971; Shideler, 1973), but the prediction remains untested in nature. One problem is that most natural mimicry complexes involve only a few, very precise mimics (Pough, 1988*b*). The range of mimics apparently protected through resemblance of coral snakes provides a situation in which to test this idea.

The differences in attack frequencies on various banded patterns suggest that some

patterns may indeed be better mimics than others. However, it is difficult to rank the patterns in similarity to the model because there are probably multiple models (at least 2 to 3 patterns of elapid coral snakes) and the stimulus components important for recognition of coral snake patterns by birds are unknown. Nonetheless, this study establishes that relative mimetic advantage varies among protected banded patterns. Further experimentation of this type, especially at localities with only a single model pattern, may elucidate this problem.

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