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*Functional Ecology*, Vol. 9, No. 2 (Apr., 1995), 186-190.

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# Experimental studies of Coral Snake mimicry: generalized avoidance of ringed snake patterns by free-ranging avian predators

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## Summary

1. Plasticine snake replicas were used to demonstrate that free-ranging avian predators generalize avoidance of Coral Snake ringed patterns to similar patterns, supporting the argument that the convergence on ringed and banded patterns among neotropical snakes is a result of the mimetic advantage of resembling venomous Coral Snakes.
2. The study was conducted at a tropical dry forest site in Costa Rica, where only one species of Coral Snake occurs. The Coral Snake has a tricolour (red–yellow–black–yellow–red) ringed pattern and no snakes at the site have bicolour (red–black) ringed patterns. Neither tricolour nor bicolour ringed replicas were attacked by birds, whereas an unmarked brown replica was.
3. The avoidance of the bicolour ringed pattern is attributable to generalized avoidance of Coral Snake-like patterns. No red-and-black ringed prey have been observed at the site, so birds could not have learned specific avoidance of the bicolour pattern. Historical biogeographical evidence suggests that the avifauna at the site did not evolve in the presence of red-and-black ringed snakes, so it is unlikely that birds evolved a specific innate avoidance of the bicolour ringed pattern.

*Key-words:* Adaptive coloration, antipredator mechanisms, aposematism, innate avoidance behaviour, *Micrurus*

*Functional Ecology* (1995) **9**, 186–190

## Introduction

The conspicuous resemblance between venomous elapid Coral Snakes (*Micrurus* and *Micruroides*) and a variety of mildly or non-venomous colubrid snakes has long been recognized (Cope 1860; Wallace 1870) and has often been cited as a classical example of mimicry among vertebrates (Wickler 1968; Greene & McDiarmid 1981; Pough 1988a,b). This explanation of the convergent evolution of bright (red, yellow and black) ringed patterns in neotropical snakes has resulted in much controversy, but comparative and experimental evidence has generally supported such an interpretation (but see Vitt 1992). Although many of the key arguments against Coral Snake mimicry have been refuted, we still know little about how Coral Snake mimicry systems operate in nature.

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Field experiments have demonstrated that free-ranging birds avoid all ringed patterns found on sympatric snake species in a Costa Rican rain forest. Because each of these patterns could have been encountered on real prey, it is impossible to determine whether ringed patterns are protected because they resemble Coral Snake patterns or because each represents a specific unfavourable prey item (Brodie 1993). Studies with naive captive birds (*Eumomota superciliosa* and *Pitangus sulphuratus*) suggest that at least two potential snake predators innately avoid true Coral Snake and similar patterns (Smith 1975, 1977). However, the non-Coral Snake patterns used in those experiments included elements (e.g. green and blue rings) not found on any extant snake species or other potential prey item, and may represent avoidance of unnatural novel stimuli. A wealth of indirect evidence from parallel geographical variation in colour pattern of neotropical snakes to the number of snake species that exhibit red coloration in sympatry with members of the genus *Micrurus*, also suggests that there is some mimetic advantage to resembling venomous

Coral Snakes (Greene & McDiarmid 1981; Pough 1988a,b). None of these studies has demonstrated that free-ranging predators generalize their avoidance of Coral Snake ringed patterns to similar colour patterns found in nature. This point remains central to understanding the evolution of these unique mimicry complexes.

Investigations of Coral Snake mimicry in nature are hampered by two primary features of neotropical snake assemblages. First, most areas are inhabited by multiple species of ringed snakes, usually including several species of venomous Coral Snakes with different colour patterns (Campbell & Lamar 1989). This variety of potential models obfuscates relationships between model and mimic patterns. Second, encounter rates with any single snake species are low (e.g. Zimmerman & Rodriguez 1990), making observations of interactions between predator and prey serendipitous at best. This latter problem can be circumvented by using soft plasticine replicas to survey predation attempts on a large number of subjects simultaneously because replicas retain impressions in their surfaces from any disturbances (Madsen 1987; Brodie 1993).

We used plasticine snake replicas to survey avian predation on different colour patterns at a tropical dry forest site in western Costa Rica. This study site differs from those previously studied in that it is inhabited by a single species of Coral Snake and a few mimics, so several colour patterns common in other neotropical snake assemblages are not present (Savage & Vial 1974; Campbell & Lamar 1989). The resident coral snake, *Micrurus nigrocinctus*, has a tricolour ringed pattern [red–yellow–black–yellow–red, the ‘monad’ of Savage & Slowinski (1992)]. Several other non- or mildly venomous colubrids in this area have tricoloured ringed patterns and are considered Coral Snake mimics, including *Erythrolampis bizona*, *Lampropeltis triangulum* [both with red–black–yellow–black–red tricolour ‘dyads’ of Savage & Slowinski (1992)] and *Scolecophis atrocinctus* [white and black rings with a red dorsal stripe, the ‘TZ’ pattern of Savage & Slowinski (1992)] (Savage & Vial 1974; Campbell & Lamar 1989). No snake in this region has a bicolour ringed pattern of red and black, a pattern found on both Coral Snakes and mimics in other parts of the neotropics (Savage & Vial 1974; Savage & Villa 1986; Campbell & Lamar 1989; Brodie 1993). We made replicas of the tricolour ringed Coral Snake pattern, a red and black ringed pattern and an unmarked brown control to determine if free-ranging birds generalize avoidance of a Coral Snake pattern (tricolour ringed) to a similar snake pattern (bicolour ringed) that they have not previously experienced.

### Materials and methods

Snake replicas were constructed using precoloured,

non-toxic plasticine (Sculpey-III modelling compound) (Brodie 1993). Ringed patterns were reproduced by threading cylindrical slices of different colours on to an S-shaped wire to produce a replica 1 cm in diameter and 16 cm in length. Lengths of wire (3 cm) were left protruding at each end of the replica and were used to anchor it to the ground. Three colour patterns were used: the tricolour ringed pattern of the local *Micrurus nigrocinctus*, the red and black ringed pattern of *Micrurus multifasciatus* from the Atlantic lowlands of Costa Rica, and an unmarked brown pattern representing a number of non-venomous colubrid and anniliid snakes present in the area. The colour patterns we replicated were based on our personal experiences with and photographs of living individuals of all taxa.

Sixty of each replica type were placed in each of two transects for a total of 120 replicas per pattern and 360 replicas overall. The two transects were simultaneously placed approximately 2 km apart along existing trails through secondary tropical dry forest at the Palo Verde Biological Station (Organization for Tropical Studies), Guanacaste Province, Costa Rica on 14–16 February 1992. Replicas were placed 0.5 m from the edge of the trail at 10 m intervals in randomized orders. After 48 h, replicas were surveyed for marks and collected.

The approximate size and shape of each mark was noted. Replicas with more than one mark (of the same type) were scored as a single disturbance, because of the probability that these multiple marks came from a single event. A few replicas could not be relocated. These were conservatively scored as undisturbed because of the possibility that we simply failed to find them.

Analyses were performed using *G*-tests (Sokal & Rohlf 1981). We added one to all cells with zero counts to be able to calculate *G*-statistics (because the  $\ln$  of zero is undefined). Such a procedure deflates the *G*-statistic and will lead to conservative conclusions. Statistical significance was judged at  $P < 0.05$ .

### Results

Agents of disturbance were easily recognizable from the impressions left on the replicas. Birds left characteristic paired V- or U-shaped marks on opposite sides of replicas. It has been demonstrated previously that such beak imprints represent predation attempts (Brodie 1993). No avian attacks were directed towards either of the ringed replica types (Fig. 1). The difference in frequency of avian attacks between the unmarked brown control and the ringed patterns was statistically significant ( $G = 9.475$ ,  $P < 0.01$ ,  $df = 2$ ).

Non-avian disturbances included ants, human bootprints, rodents and some larger mammals (probably didelphids, based on the size and type of toothmarks). Because these agents were not predators, or were unlikely to be visually orientated foragers, these

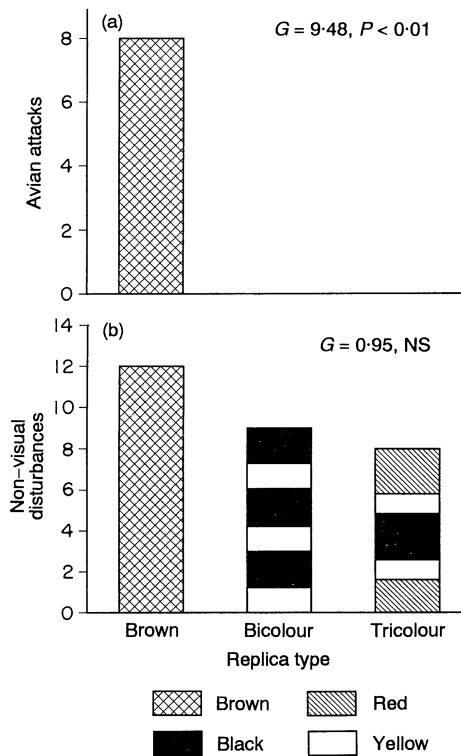


Fig. 1. Number of avian attacks (a) and non-visual disturbances

marks were considered non-visual disturbances. A number of replicas were bitten by lizards, primarily *Ctenosaura similis*, a large herbivorous iguanid. These lizards are diurnal, visual foragers but are unlikely to be predators of snakes. Lizard disturbances were not, therefore, included as either visual attacks or non-visual disturbances [these data are discussed elsewhere (Janzen & Brodie 1995)]. Non-visual disturbances were distributed randomly among the pattern types (Fig. 1;  $G = 0.953, NS, df = 2$ ), indicating there was no bias toward encountering the brown pattern inherent in the construction or placement of the replicas.

## Discussion

The ringed patterns of both sympatric and allopatric species of Coral Snakes were avoided by avian predators. A previous experiment indicates that a non-moving tricolour ringed pattern is not more cryptic than an unmarked brown pattern (at least in rain forest understory), and that differences in frequency of avian attacks between brown and ringed models are a result of active avoidance (Brodie 1993).

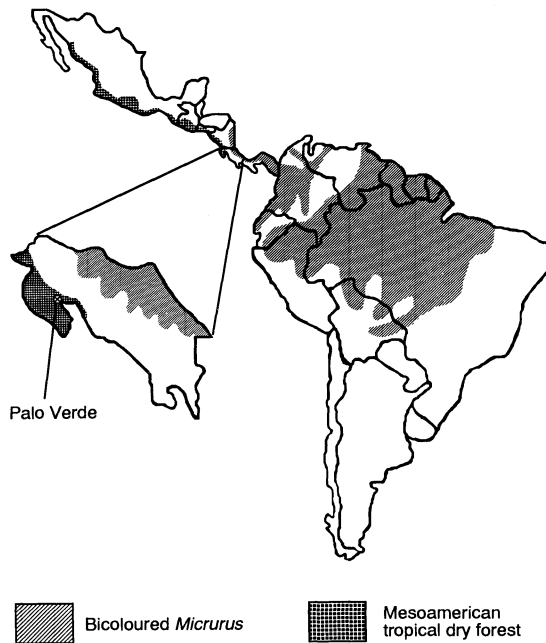
Avoidance of the red and black ringed pattern by the avian predator community at Palo Verde could represent either a specific response to that pattern or a generalized aversion to brightly ringed patterns.

Predators could have developed a specific aversion to a red and black ringed pattern by: (1) avoidance learned through individual experience; or (2) innate avoidance that evolved because of ancestral experience with such prey. It is unlikely that the individual predators sampled in our study had ever experienced red and black ringed prey. With the exception of migrating water birds (which were not exposed to the replicas in this experiment), virtually all the potential avian predators on reptiles at the study site during February are resident species (Stiles 1983; Stiles & Skutch 1989). Red and black ringed patterns are not found on any snakes at the study site and no other elongate prey with such a pattern (e.g. millipedes, cf. Vitt 1992) have been observed there (M. Quesada & K. Stoner, personal communication). Thus, it is improbable that any of the birds that encountered our replicas had experienced previously such red and black ringed prey.

The second possibility, that predators have evolved a specific congenital avoidance of red and black patterns because of experience (and therefore selection) during their evolutionary histories, is more difficult to discount. Innate avoidance of Coral Snake ringed patterns has been demonstrated for avian and mammalian predators (Gehlbach 1972; Smith 1975, 1977). For such a phenomenon to have evolved, the modern avian predator lineages at Palo Verde must have been sympatric with red and black ringed prey at some time during the past, and encounters with those prey must have been sufficiently detrimental to result in selection against individuals that attacked them. Venomous snakes are one of the few prey that could represent such a selective pressure (Pough 1988b). Historical biogeographical and phylogenetic evidence suggest that the necessary conditions for such an evolutionary scenario never existed.

The avifauna of the Palo Verde region is the southernmost extension of the tropical dry forest avifauna that ranges north to Sonora, Mexico along the Pacific coast (Stiles 1983). These taxa are thought to be primarily of North American origin (Fig. 2) (Stiles & Skutch 1989). The dry forest avifauna shares few taxa with other regions of Costa Rica and most of these species probably have secondarily invaded disturbed areas in these other life zones (Stiles 1983). Thus, the avian predator lineages at Palo Verde most likely evolved with North and Central American dry forest prey communities.

Elapid Coral Snakes (*Micrurus* spp.) are also of North American origin, but are ancestrally tricolour ringed. The bicolour ringed pattern apparently evolved in a predominantly South American clade and also in a few isolated populations and species in Mexico and northern Central America (Campbell & Lamar 1989; Slowinski 1991). The current distribution of the bicoloured species in Central America is a reinvasion of that region by the bicoloured South American clade, and extends only along the Atlantic



**Fig. 2.** Map of Mexico, Central and South America with Costa Rica enlarged showing the historical distribution of the Mesoamerican tropical dry forest avifauna (cf. Stiles 1983; Stiles & Skutch 1989) and the modern distribution of red and black bicoloured Coral Snakes (*Micrurus* sp.) (cf. Campbell & Lamar 1989). Note that the distributions of the two do not overlap, suggesting that the Mesoamerican tropical dry forest avifauna did not experience bicoloured Coral Snakes during their evolutionary history.

coast of Costa Rica (Fig. 2). The range of bicoloured taxa does not overlap with the range of the tropical dry forest life zone (Campbell & Lamar 1989; Slowinski 1991).

It is likely, then, that the dry forest avifauna did not evolve in the presence of bicoloured Coral Snakes and therefore did not evolve a specific innate avoidance of red and black ringed patterns, though we cannot rule out the possibility that specific avoidance arose through interaction with other elongate, red and black ringed prey such as millipedes (cf. Vitt 1992). We believe that the avoidance of red and black ringed replicas in this experiment is best explained as generalized avoidance of ringed patterns by avian predators of snakes. This interpretation is supported by studies of captive naive birds that avoided red and yellow ringed and red, yellow and black striped dowels (Smith 1975, 1977). Neither of these colour schemes is found on any living snake taxon, so such responses were probably general aversions to other patterns. Pough (1988b) has further argued that the severe consequences of attacking venomous snakes results in very general avoidance, possibly of all snake-like forms. Our study suggests that an entire assemblage of free-ranging avian predators does in fact generalize avoidance of a venomous snake.

## Acknowledgements

We thank the Organization for Tropical Studies, N. Grieg, M. Morris and the participants of OTS 92-1 for help and support in all aspects of this study. Financial support to E.D.B.III was provided by the Miller Institute for Basic Research in Science. E.D. Brodie, Jr, H. Greene and J.A. Rodriguez-Robles provided comments on the experimental design and/or manuscript.

## References

- Brodie E.D. III, (1993) Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. *Evolution* **47**, 227–235.
- Campbell, J.A. & Lamar, W.W. (1989) *The Venomous Reptiles of Latin America*. Cornell University Press, Ithaca.
- Cope, E.D. (1860) Catalogue of the Colubridae in the Museum of the Academy of Natural Sciences of Philadelphia, with notes and descriptions of new species. *Proceedings of the Academy of Natural Sciences, Philadelphia* **12**, 241–266.
- Gehlbach, F.R. (1972) Coral snake mimicry reconsidered: the strategy of self-mimicry. *Forma et Functio* **5**, 311–320.
- Greene, H.W. & McDiarmid, R.W. (1981) Coral snake mimicry: does it occur? *Science* **213**, 1207–1212.
- Janzen, F.J. & Brodie, E.D., III (1995) Visually-oriented foraging in a natural population of herbivorous lizards (*Ctenosaura similis*). *Journal of Herpetology* **29**, 132–136.
- Madsen, T. (1987) Are juvenile grass snakes, *Natrix natrix*, aposematically coloured? *Oikos* **48**, 265–267.
- Pough, F.H. (1988a) Mimicry and related phenomena. *Biology of the Reptilia, vol. 16, Defense and Life History* (eds C. Gans & R. B. Huey), pp. 153–234. Alan R. Liss, Inc., New York.
- Pough, F.H. (1988b) Mimicry of vertebrates: are the rules different? *American Naturalist* **131**, S67–S102.
- Savage, J.M. & Slowinski, J.B. (1992) The colouration of the venomous coral snakes (family Elapidae) and their mimics (families Aniliidae and Colubridae). *Biological Journal of the Linnean Society* **45**, 235–254.
- Savage, J.M. & Vial, J.L. (1974) The venomous coral snakes (genus *Micrurus*) of Costa Rica. *Revista de Biología Tropical* **21**, 295–349.
- Savage, J.M. & Villa, J. (1986) *Herpetofauna of Costa Rica*. Society for the Study of Amphibians and Reptiles, Athens.
- Slowinski, J.B. (1991) *The phylogenetic relationships of the new world coral snakes (Elapidae: Leptomicrurus, Micruroides and Micrurus) based on biochemical and morphological data*. Unpublished PhD thesis, University of Miami, Miami, FL.
- Smith, S.M. (1975) Innate recognition of coral snake pattern by a possible avian predator. *Science* **187**, 759–760.
- Smith, S.M. (1977) Coral-snake pattern recognition and stimulus generalisation by naive great kiskadees (Aves: Tyrannidae). *Nature* **265**, 535–536.
- Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*. W. H. Freeman and Company, New York.
- Stiles, F.G. (1983) Birds. *Costa Rican Natural History* (ed. D. H. Janzen), pp. 502–530. University of Chicago Press, Chicago.

- Stiles, F.G. & Skutch, A.F. (1989) *A Guide to the Birds of Costa Rica*. Cornell University Press, Ithaca, NY.
- Vitt, L.J. (1992) Lizard mimics millipede. *National Geographic Research and Exploration* **8**, 76–95.
- Wallace, A.R. (1870) *Contributions on the Theory of Natural Selection*. Macmillan & Co., London.
- Wickler, W. (1968) *Mimicry in Plants and Animals*. Weidenfeld & Nicolson, London.

- Zimmerman, B.L. & Rodrigues, M.T. (1990) Frogs, snakes, and lizards of the INPA-WWF reserves near Manaus, Brazil. *Four Neotropical Forests* (ed. A. H. Gentry), pp. 426–454. Yale University Press, New Haven.

*Received 29 November 1993; revised 18 July 1994; accepted 29 July 1994*