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Experimental studies of coral snake mimicry: do snakes mimic millipedes?

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The prevalence of similarly ringed colour patterns in Neotropical snake species has stimulated heated controversy over the cause of this apparent convergence since it was first noted by Cope (1860) and Wallace (1870) in the last century. These ringed and banded species include venomous (neurotoxic) elapid coral snakes (*Micrurus*) and a number of mildly or non-venomous colubrid and anniliid snakes. The most commonly accepted explanation for this convergence in colour pattern is coral snake mimicry (Greene & McDiarmid 1981; Pough 1988). This hypothesis, wherein the non-elapid species are protected through resemblance of the true coral snakes, is now supported by comparative and laboratory and field experimental evidence (Smith 1975, 1977; Greene & McDiarmid 1981; Pough 1988; Campbell & Lamar 1989; Brodie 1993; Brodie & Janzen, in press). However, there are still untested alternatives to the coral snake mimicry hypothesis, including convergence on a common colour pattern because of crypsis or aposematism for unprofitability as prey, or even selective neutrality of ringed patterns (for a recent review, see Pough 1988). Perhaps the strongest alternative explanation is that all ringed or banded snakes (and lizards) may actually be mimics of other banded elongate animals such as millipedes (Vitt 1992). Most Neotropical ringed snakes are slender, and even as adults are similar in diameter to large millipedes (e.g. Campbell & Lamar 1989). The argument has been made that millipedes are commonly banded, produce toxic compounds for defence (Eisner et al. 1978), are locally common throughout the tropics and share predators in common with small reptiles. Experimental evidence suggests that some captive birds and mammals learn to avoid millipedes after experiencing their noxious secretions (Eisner et al. 1978). Additionally, millipedes have been present during the entire evolution of vertebrates (since the Silurian; Almond 1985), and thus could represent the original model for mimicry systems involving elongate ringed or banded prey (Vitt 1992).

Before the 'millipede as model' hypothesis can be evaluated, some basic data must be collected. At present, no information is available on the frequency of predation by visual predators on ringed millipedes, or on the ability of such predators to distinguish between patterns exhibited by millipedes and those found on snakes. To argue that millipedes are the true model for coral snake mimicry complexes, it must be established that (1) millipedes and snakes have visual predators in common, (2) visually foraging predators avoid millipedes and (3) these predators do not distinguish between millipede and snake ringed patterns.

We conducted a field experiment to determine whether millipedes are avoided by free-ranging, visually foraging predators (birds, see below) and if such predators distinguish between the ringed patterns found on snakes and millipedes. We constructed plasticine millipede-sized models that differed only in coloration. Models were then exposed to predation attempts by free-ranging birds to determine the relative attack frequency on models with different colour patterns. The techniques and materials used to produce the models are described elsewhere (Brodie 1993; Brodie & Janzen, in press). Three patterns were tested (Fig. 1): unmarked brown, red and black narrow ringed ('millipedes'), and red and black wide ringed ('coral snakes'). The two ringed patterns differed only in ring width, one corresponding to ring widths found on the bicolour coral snake in the study area (*Micrurus multifasciatus*; Campbell & Lamar 1989), the other corresponding to ring widths characteristic of ringed millipedes

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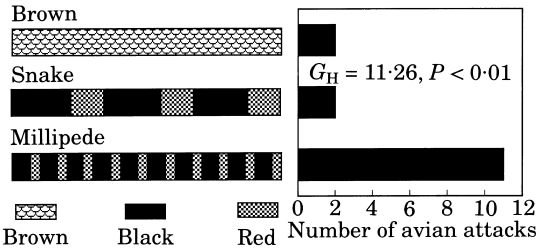

Figure 1. Colour patterns of the three model types used and the number of avian attacks on each type (out of 50 models each). Significantly more millipede patterned models were attacked than either the coral snake or unmarked brown patterns.

(modelled after an unidentified pink and black millipede that has been observed at the study site and photos of several species of the Central American banded genus *Rhinocricus* in Vitt 1992). The 'millipede' models had 0·5 cm black and 0·25 cm red rings, while the 'coral snake' models had 1·7 cm black and 0·8 cm red rings (Fig. 1). These ring widths provided two patterns identical in the total amount of red and black in each, as well as identical relative widths (2:1) of black and red rings. Models were constructed to be millipede size (7·5 cm long × 0·75 cm in diameter). If mimicry operates between ringed snakes and millipedes, both ringed patterns should be attacked less often than the unmarked brown.

Twenty-five models of each pattern type were placed in each of two transects, for a total of 50 models per pattern, 150 models total. Transects followed existing trails at the La Selva Biological Station, Costa Rica (a lowland Atlantic rainforest site), and were placed approximately 2 km apart. The two transects were conducted sequentially, between 18 and 23 March 1994. Models were placed individually at 10-m intervals in a randomized order. After 48 h, we surveyed replicas for marks and collected them (cf. Brodie 1993; Brodie & Janzen, in press). We noted the size and shape of each mark. No model had multiple marks. Only marks left by birds, assessed by V- or U-shaped imprints in the plasticine (see photos in Brodie 1993), were assumed to result from visually oriented predation attempts (see Brodie 1993; Brodie & Janzen, in press). Only these marks are discussed further. We tested differences in attack frequencies by a goodness-of-fit test (Sokal & Rohlf 1981).

The distribution of predation attempts among the three model types was decidedly non-random (Fig. 1). Millipede models had significantly more bill imprints than either of the other two models ($G_H = 11{\cdot}26$, $df = 2$, $P < 0{\cdot}01$). In fact, 22% of the millipede models were attacked, almost twice the frequency reported for an unmarked brown model of snake size used in a previous experiment at the same locality (12%; Brodie 1993). It is also notable that the unmarked brown model in this experiment received fewer attacks than the millipede pattern, but no more than the coral snake pattern. Bill imprints in all models were qualitatively similar to those found in similar studies (Brodie 1993; Brodie & Janzen, in press).

These results suggest that ringed millipedes are not generally avoided by avian predators. Some species of birds may avoid millipedes, but these obviously would not have attacked the millipede models in this experiment. It is also possible that predators in other parts of the Neotropics may avoid millipedes, but at least in the Atlantic lowlands of Costa Rica there does not appear to be a widespread aversion to ringed millipede patterns among birds.

The difference in attack frequency between the millipede and coral snake ringed models is noteworthy because it indicates that birds are able to distinguish between patterns on the basis of ring width alone. All elements of the two models were identical (see above) except that the millipede pattern had narrower rings. Previous experiments demonstrated that a wide range of ringed patterns were avoided by avian predators (Brodie 1993). These patterns were presented on larger models (1 × 16 cm), and it is possible that an interaction between size and pattern yields different responses. This would have to be directly tested using the same pattern on models of different size.

This study does not support the view that millipedes are models for coral snake mimicry systems. This sort of contemporary experiment cannot address the historical argument that ringed millipedes were the original models for mimicry systems involving ringed or banded reptiles (Vitt 1992). However, it is noteworthy that the ancestral colour pattern of coral snakes is tricolour-ringed (Slowinski 1991), yet no tricolour ringed millipedes are known in the Neotropics. Furthermore, the only radiation of tricolour ringed or banded snakes of other taxa (i.e. 'mimics') appears to have occurred in sympatry with true

coral snakes (Greene & McDiarmid 1981; Pough 1988). Patterns or colours of the early millipedes can only be guessed (colour does not fossilize) and may have changed. Species and distributions of visual predators may have changed since the radiations of Neotropical ringed snakes. None the less, the current lack of avoidance of millipede width rings suggests that even if millipedes were avoided by some predators in the past, the present Costa Rican rainforest avifauna does not avoid ringed and banded snake patterns because of a generalized avoidance of millipedes. In fact, this study cannot rule out the possibility that ringed millipedes gain some mimetic advantage from their resemblance of coral snakes.

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