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## Wallace and Savage: Heroes, Theories, and Venomous Snake Mimicry

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In the dawn of field biology, Alfred Russel Wallace departed for the most distant and dangerous biotic frontiers of the world, carrying with him little formal education but a blessed love of reading and reflective solitude. He sought the insect-ridden Edens of which naturalist explorers dream. His principal lifeline to the English homeland consisted of specimens outbound—birds skinned, insects pinned, plants pressed—and sporadic payments for his treasures inbound. An intense young man, totally focused, awesomely persistent and resourceful, resilient to tropical diseases that might have killed others, and nobly selfless, even to Darwin, who otherwise might have become a bitter rival, Wallace endured, and he triumphed. He succeeded brilliantly because he relished detail while thinking across a wide canvas.

E. O. WILSON (1999)

Among the Bribri, Cabécar, Boruca, Changina, and Chiriquí, when the chicha has been drunk, the night grows late and dark, and the fires die down to burning embers, the wisest old man of the tribe tells his engrossed listeners of a beautiful miraculous golden frog that dwells in the forests of these mystical mountains. According to the legends, this frog is ever so shy and retiring and can only be found after arduous trials and patient search in the dark woods on fog shrouded slopes and frigid peaks. However, the reward for the finder of this marvelous creature is sublime. Anyone who spies the glittering brilliance of the frog is at first astounded by its beauty and overwhelmed by the excitement and joy of discovery. . . . The story continues that those who find the legendary frog find happiness, and as long as they hold the frog happiness will follow them everywhere. . . . Field biologists in particular seem always to be searching for mystical truth and beauty in nature, and frequently at some unperceived level, for the happiness promised by the Indian seers.

J. M. SAVAGE (1970)

The mysteries of mimicry had a special attraction for me. . . . “Natural selection” could not explain the miraculous coincidence of imitative aspect and imitative behavior, nor could one appeal to the theory of “the struggle for life” when a protective device was carried to the point of mimetic subtlety, exuberance, and luxury far in excess of a predator’s power of appreciation. I discovered in nature the nonutilitarian delights that I sought in art. Both were a form of magic, both were a game of intricate enchantment and deception.

VLADIMIR NABOKOV (QUOTED IN BOYD AND PILE 2000)

In this chapter, we honor Alfred Russel Wallace and Jay Mathers Savage by discussing venomous snake mimicry, a topic about which they each made fundamental discoveries. As field biogeographers, these men have focused on organisms in nature and thereby contributed to the conceptual advancement of evolutionary biology; each of them also has been outspoken in defense of nature against the onslaught of human activities. We especially admire Wallace for pushing the frontiers of nineteenth-century natural history, for his gracious attitude toward Charles Darwin in the face of their co-discovery of natural selection, and for brilliantly synthesizing across animals as different as insects, carnivores, and snakes (see Quammen 1996; Daws and Fujita 1999; Raby 2001). We praise Savage for flouting traditional boundaries between art and science, for his joyous loyalty to students and friends, and for pursuing the biology of amphibians and reptiles against the backdrop of landscape history, thereby inspiring so many of us to reach higher and farther.

Theories tell us what we know, they suggest where to look and what to measure next, and they encapsulate the state of science. Most of us study nature better when we are guided by theory, and the essence of “the” scientific method is testing alternative hypotheses, ideally via controlled experiments. Nonetheless, organisms are the fundamental packages in which life varies, reproduces, and persists; they are the functioning arenas in which behavioral, physiological, and morphological systems are organized as well as the living building blocks of populations, communities, ecosystems, and biomes (Brooks 2001). Biologists ultimately seek to understand the lives of organisms and patterns of their diversification—not theories and experiments—and thus discoveries of new kinds of organisms and new things about organisms chronically reset the “research cycles” (Kluge 1991) of hypothesis testing that underlie good, progressive science.

In this chapter, we update Pough's (1988a) review of venomous snake mimicry and then show how recent discoveries might modify previous conclusions. Next we describe four macroevolutionary patterns, recognition of which ultimately stems from studies of coralsnake mimicry, and name them for Wallace and Savage. Then we comment on some unanswered questions and promising avenues for future research. By revisiting venomous snake mimicry, we hope to illustrate that in spite of an emphasis in modern science on hypothesis testing and generalization, organisms themselves should always be a central focus of biology (Greene 1986; West-Eberhard 2001). And recalling Nabokov's skeptical comments, quoted in one of the epigraphs at the beginning of this chapter, we take pleasure in linking our two visionary heroes with a phenomenon of such obvious aesthetic as well as scientific appeal. It turns out that in the case of venomous snake mimicry, things may not be quite as they have seemed.

### *Coralsnake Mimicry Revisited*

This beautiful species [*Pliocercus elapoides*] resembles in the distribution of its colors certain Elapses [*sic*, venomous coralsnakes]. . . . It is a beautiful example of analogy of coloring.

E. D. COPE (1860)

In the Vertebrata . . . external form depends almost entirely on the . . . skeleton . . . [and] cannot therefore be rapidly modified by variation. . . . We can hardly see the possibility of a mimicry by which the elk could escape from the wolf, or the buffalo from the tiger. There is, however, in one group . . . such a general similarity of form, that a very slight modification, if accompanied by identity of colour, would produce the necessary amount of resemblance; and . . . there exist . . . species which it would be advantageous to resemble, since they are armed with the most fatal weapons of offence. We accordingly find that reptiles furnish us with a very remarkable and instructive case of true mimicry.

A. R. WALLACE (1870)

#### THE FIRST CENTURY OF CORALSLNAKE MIMICRY

Although Cope (1860, as quoted in an epigraph above) is sometimes credited with first calling attention to coralsnake mimicry, by "analogy" he implied only some shared, unstated function for the external resemblance of his new species of colubrid to venomous coralsnakes (Elapidae). Cope's comments were made shortly before Bates (1862) proposed the concept of mimicry, in which a predator (dupe) avoids a palatable prey (mimic) that it mistakes for an unpalatable species (model) as the result of similar attributes of the latter two organisms. As young men, Wallace and Bates had traveled together in the Neotropics, and the

former first clearly described as mimicry the resemblances between non-venomous colubrids and dangerous elapids (Wallace 1867; reprinted and slightly revised in Wallace 1870). Among Wallace's examples of parallel geographic variation in Batesian mimics and models are snake taxa we later analyzed in more detail (Greene and McDiarmid 1981), including the colubrid *Pliocercus* (= *Urotheca*, Savage and Crother 1989), and Wallace (1867) also first offered a compelling explanation for why mimicry is generally rare among vertebrates but common among snakes.

For about a hundred years after Wallace's (1867) report, discussions of the "coralsnake mimicry problem" concerned primarily similarities between venomous elapids and supposedly harmless species (reviewed in Pough 1988a). Early proponents relied on observations of museum specimens and organisms in nature rather than on experiments, and their opponents often resorted to unsubstantiated arguments and assertions. Dunn (1954), Mertens (1956), and Wickler (1968) analyzed model-mimic abundance ratios with the expectation that, because predators will only avoid color patterns if they are usually associated with unpleasant consequences, mimics must be relatively rare. Those data sets were problematic, however, because of difficulties in assessing the availability of snakes to predators, and we now know that interpreting model-mimic ratios is at best complex (Mallet and Joron 1999). Better evidence that a widespread South American colubrid clade (*Erythrolamprus*) does mimic sympatric elapids came from lack of a coralsnake pattern in *Erythrolamprus ocellatus* on Tobago, an island off Trinidad, where there are no venomous models (Emsley 1966; photos in Boos 2001). Critics meanwhile claimed that fatal elapid bites would preclude learning by predators (the "deadly model problem") and that supposedly nocturnal coralsnakes are not accessible to predators with color vision. In fact, the consequences for predators that attack venomous snakes can range from mild discomfort to death (Emsley 1966; Pough 1988a, 1988b). Even early reports documented diurnality in coralsnakes and their presumptive mimics (Strecker 1927; Greene and McDiarmid 1981; Sazima and Abe 1991; Martins and Oliveira 1993, 1998; Gurrola-Hidalgo and Chavez C. 1996; Savage and Slowinski 1996; Smith and Chiszar 1996; Stafford 1999), and color vision is reasonably widespread among vertebrates (e.g., Loop and Crossman 2000).

A frequently expressed alternative to the coralsnake mimicry hypothesis (e.g., Gadow 1911; Brattstrom 1955; Sánchez-Herrera et al. 1981), that similar color patterns were convergently acquired in response to some environmental factor other than predator signaling, is in hindsight surprisingly easy to dismiss. Although independent evolution of similar external appearance among snake species is common, pairs of such taxa generally fall into two groups: those that are ecologically similar but widely allopatric (e.g., the Emerald Tree Boa, *Coralus caninus*, of the Amazon Basin; and Green Tree Python, *Morelia viridis*, on New Guinea), as predicted by the competitive exclusion principle, and those in

which one or both members of the pair are venomous and they are sympatric, as expected for mimicry (Greene 1997). A variant of the coralsnake mimicry hypothesis, that brightly colored colubrids escape predation when similarly patterned venomous elapids mistake them as conspecifics, also seems unlikely for these primarily chemosensory organisms. There are numerous records of intrageneric and even intraspecific predation by *Micrurus* (Roze 1996), as well as of predation by those venomous coralsnakes on the presumptive mimics *Cemophora coccinea* (by *M. fulvius*, Heinrich 1996), *Hydrops triangularis* (by *M. lemniscatus*, Roze 1996), *Leptodeira nigrofasciata* (by *M. nigrocinctus*, E. D. Brodie III, pers. comm.), and *Urotheca elapoides* (by *M. bernadi*, Roze 1996; *M. diastema*, H. W. Greene, unpub. obs.). At least one mildly venomous colubrid (*Erythrolamprus aesculapii*) occasionally preys on another (*Oxyrhopus guibei*, Sazima and Abe 1991). In any case, coralsnake mimicry's first century closed with Wickler's (1968) semipopular summary of the problem and a lack of convincing consensus.

#### PROGRESS AND SYNTHESIS

Twenty years ago we attempted to clarify the coralsnake mimicry problem by distinguishing two questions, of which only the second was dependent on a particular answer to the other: Are color patterns and defensive behaviors of certain venomous snakes aposematic, and are species that resemble those dangerous models in fact mimics (Greene and McDiarmid 1981)? Most early objections to mimicry (e.g., erroneous claims that the models are nocturnal and always deadly) actually had focused on the first question, whereas evidence from model-mimic ratios supposedly dealt with the second (e.g., Dunn 1954; Mertens 1956). Subsequent to Wickler's (1968) review, experimental studies on possible mammalian predators (Gehlbach 1972) and predatory Neotropical birds (Smith 1975, 1977) had addressed aposematic coloration in venomous coralsnakes rather than mimicry per se. In particular, Smith used wooden model snakes to separately control for color and pattern, and thus decisively solved the deadly model problem; she proved that naive individuals of relevant predators do avoid coralsnake color patterns and therefore need not learn the significance of those patterns to avoid harmless mimics. Building on Savage and Vial's (1974) study of Costa Rican coralsnakes, we documented concordant geographic color pattern variation in several putative Batesian mimics (*Atractus*, *Erythrolamprus*, *Lampropeltis triangulum*, and *Urotheca elapoides*) with respect to sympatric elapids (Greene and McDiarmid 1981), and thus supported the hypothesis that certain harmless or mildly venomous colubrids are indeed Batesian mimics of deadly elapids. Moreover, *Micruroides euryxanthus* closely resembles a larger venomous coralsnake, *Micrurus distans*, in color pattern only where they are sympatric, implying Müllerian mimicry by those venomous elapids (Greene and McDiarmid 1981).

Smith's (1975, 1977) experiments and our 1981 paper evidently sparked an attitudinal shift among herpetologists in favor of coralsnake mimicry (e.g., cf. Sánchez-Herrera et al. 1981 with Smith and Chiszar 1996; but see Bauer and DeVaney 1987; Beckers et al. 1996), and Pough (1988a, 1988b) linked venomous snakes with general mimicry theory. Two subsequent decades have revealed numerous additional examples of behavioral and color pattern resemblances between colubrids and venomous elapids, reasonably viewed as putative Batesian mimics and models, respectively (e.g., Campbell and Lamar 1989; Marques and Puerto 1991; Sazima and Abe 1991; Martins and Oliveira 1993, 1998; Roze 1996; Wilson et al. 1996; Vogt 1997; Köhler 2001; Zug et al. 2001). Additional cases of presumptive Müllerian mimicry, based on color patterns shifts by one or both venomous species where they are sympatric, include *Micrurus bocourti* and *M. mertensi*, *M. corallinus* and *M. decoratus*, *M. dissoleucus* and *M. dumerilii*, *M. frontalis* and *M. lemniscatus*, and *M. isozonus* and *M. lemniscatus* (Roze 1996; Marques 2002).

Since Pough's (1988a) review, an analysis of specimens from Brazil documented frequency shifts in alternative morphs of *Erythrolamprus aesculapii* across a parapatric range contact between it and two venomous coralsnakes with respectively similar color patterns (Marques and Puerto 1991). In local Costa Rican transects, motmots (the birds studied by Smith 1975) and other predators attacked "normal" plasticine snake models more often than they did those that looked vaguely like coralsnakes, and realistically colored coralsnake models provided even better protection (Brodie 1993; Brodie and Janzen 1995; Brodie and Moore 1995). Savage and his students forged a standardized terminology of coralsnake color patterns (Savage and Slowinski 1990) and more thoroughly documented concordant geographic variation in *Urotheca* and *Scaphiodontophis* (Savage and Slowinski 1996) with respect to sympatric venomous elapids. Beckers et al. (1996) exposed fresh-caught White-nosed Coatis (*Nasua narica*) to sympatric snakes and recorded no avoidance of and one actual attack on *Micrurus*, but their claim that research with model coralsnakes might be irrelevant is unjustified because the latter generally has focused on avian predators, controlled separately for color and pattern, and yielded clear-cut results. More recent experimental transects with plasticine models demonstrated that the advantage of a coralsnake pattern in the United States is greater in areas of sympatry with dangerous models than at sites where venomous elapids are absent (Pfennig et al. 2001).

Numerous observations confirm that the palatability spectrum of mimicry theory is continuous or at least multimodal for snakes, and that the concept of Mertensian mimicry (Wickler 1968), in which "mildly venomous" colubrids (e.g., *Erythrolamprus*) are the models and both elapids and nonvenomous colubrids are the mimics, is encompassed by a Batesian-Müllerian mimicry continuum (Emsley 1966; Greene and McDiarmid 1981; Huheey 1988; Pough 1988a, 1988b). In fact, elapid bites are not always fatal to large mammals (e.g., Russell

1967), although they can kill fairly large raptors (Brugger 1989) and even humans (Roze 1996). Moreover, some raptors that do eat rattlesnakes (*Crotalus viridis*) nevertheless prefer nonvenomous colubrids when the latter are common, suggesting that the predators assess the risk of handling dangerous snakes relative to the cost of finding harmless prey (Fitch 1949), rather than regard rattlesnakes as absolutely unpalatable. Finally, some colubrids once thought to be harmless can deliver toxic bites (e.g., *Urotheca elapoides*, Seib 1980), and nonvenomous but powerful constrictors can fatally injure a predator (see Van Heest and Hay 2000), so nonvenomous *Lampropeltis triangulum* and other “harmless” species might even serve as Batesian and/or Müllerian models. Two important implications of these observations are that venomous snake mimicry systems might span punishment levels from temporarily uncomfortable to deadly, and that avoidance mechanisms likely include diverse types of learning as well as genetically based avoidance.

We conclude that as the twentieth century closed, available evidence strongly favored the coralsnake mimicry hypothesis. Although small sample sizes and other logistical problems have limited experimental field studies on that topic, Pough’s (1988a, 1988b) emphasis on the special qualities of snake mimicry and Savage and Slowinski’s (1992) estimate that 18% of New World non-elapid snakes are coralsnake mimics implied that broader implications might be forthcoming.

### *Other Venomous Snake Mimicry Systems*

Jararacas [*Bothrops*] are not common here . . . but a non-poisonous snake indistinguishable from it in color and pattern seems to be more common. I do not know if the resemblance is based on protective mimicry of the jararaca, or if the coloration was acquired independently by both snakes as a protective resemblance to dead leaves and the like.

FRITZ MÜLLER IN AN 1893 LETTER (QUOTED IN WEST 2003)

[*A. P. catenifer sayi*] exhaled in ordinary bullsnake fashion [and] kept up a continuous rattling of its tail among the dried grass and leaves. This combination of sounds greatly resembled the rattling of *Crotalus confluentus* [= *C. viridis*] and our reaction to it was almost as though we were really in the presence of a poisonous serpent.

J. K. STRECKER (1929)

### VIPER MIMICS

Gans’s (1961b) analysis of geographic color pattern variation in African egg-eating colubrids (*Dasypeltis*) vis-à-vis sympatric vipers (e.g., *Causus*, *Echis*) inspired our study of coralsnake mimicry (Greene and McDiarmid 1981) and re-

mains the only detailed account of mimicry among Old World snakes in general and vipers in particular (for further details, see Young, Meltzer, et al. 1999). As Pough (1988a, 1988b) noted, the color patterns of most vipers and their putative mimics are obviously cryptic, such that alternative hypotheses of concealing rather than aposematic and mimetic coloration are especially plausible. Building on Pasteur's (1982) concept of abstract mimicry, Pough (1988a, 1988b) also pointed out that a generalized resemblance to vipers is relatively common, perhaps because a locally effective cryptic color pattern and behavioral similarity together can provide sufficient mimetic protection—especially given severe punishment for mistakes by predators (e.g., an unusual, sound-producing visual display by the extremely dangerous *Echis* and harmless *Dasyplittis*).

On the basis of specific behavioral and color pattern resemblances, several putative viper mimicry systems are worthy of detailed study, and many Old World catsnakes (*Boiga*, *Telescopus*) are exemplary candidates (Pough 1988a; see Schleich et al. 1996 for *Telescopus obtusus* as a behavioral mimic of *Echis*; Disi et al. 2001 for photos of *Coluber nummifer* and *Vipera palestinae*). At Tam Dao, Vietnam, freshly collected Chinese Catsnakes (*B. multitemporalis*) reacted to light touch from a human hand by assuming an exaggerated, anterior S-shaped coil and spreading the quadratomandibular joints laterally, then striking repeatedly; they so much resembled in color pattern and behavior a more frequently encountered, sympatric pitviper, the Chinese Habu (*Protobothrops mucrosquamatus*), that in the field we had difficulty distinguishing those two species without close inspection (H. W. Greene and D. L. Hardy Sr., unpub. obs.; voucher specimens in the Museum of Vertebrate Zoology, University of California, Berkeley, MVZ 226520 and MVZ 226628 to MVZ 226638, respectively). Numerous other Old World colubrids are perhaps more abstract viper mimics, and *Psammodynastes pulverulentus* has even long been known as the Mock Viper (Greene 1989).

The colubrid clade *Pituophis*, diagnosed by an epiglottal keel and loud rattle-like hissing (Young et al. 1995), probably originated in the context of rattlesnake mimicry (Sánchez-Herrera et al. 1981). Species of *Pituophis* later diversified in color pattern and behavioral ecology (Rodríguez-Robles and de Jesús-Escobar 2000) and variously resemble rattlesnakes or not in color pattern (Cope 1900; Strecker 1927; Klauber 1956; Benson 1978; Kardong 1980). Sweet (1985) analyzed crypsis and defensive behavior in *Crotalus viridis* and *Pituophis catenifer* across a California habitat gradient and concluded that the latter is at most a behavioral mimic of the former. He also noted that color pattern classes of *Pituophis* in the eastern United States (e.g., Black Pinesnakes, *P. melanoleucus lodingi*) resemble rattlesnakes even less than do their western North American congeners, but perhaps that is because sympatric pinesnakes and Eastern Diamond-backed Rattlesnakes (*C. adamanteus*) often occupy tortoise burrows, so that the former profits primarily from acoustic rather than visual mimicry of the latter.

In response to a predator, Fox Snakes (*Elaphe vulpina*) and many other colubrids vibrate their tails and thereby might resemble rattlesnakes, and perhaps tail vibration by some Old and New World colubrids arose as behavioral mimicry of pitvipers (e.g., Cooper 1859; Hay 1892; Greene 1988, 1997; see sonograms in Kuch 1997a). Other potential North American viper mimics include the Mexican Alpine Blotched Gartersnake (*Thamnophis scalaris*), which has a color pattern reminiscent of sympatric Lance-headed Rattlesnakes (*Crotalus polystictus*), and the Mesoamerican Highlands Gartersnake (*Thamnophis fulvus*), which resembles Godman's Pitviper (*Cerrophidion godmani*) in color pattern and defensive behavior (H. W. Greene, unpub. obs. of *T. fulvus* in Guatemala, voucher specimens at the University of Texas at Arlington; photos of *Thamnophis* in Rossman et al. 1996; photos of *C. godmani* and *C. polystictus* in Campbell and Lamar 1989).

Most species of snail- and slug-eating snakes (*Dipsas*, *Sibon*, *Sibynomorphus*, the dipsadinine colubrids) probably are at least abstract mimics of terrestrial vipers, by virtue of similar cryptic color patterns and defensive displays (Peters 1960; Greene and McDiarmid 1981; Sazima 1992; Martins 1996; Martins and Oliveira 1998; Marques et al. 2001, fig. 40; Cadle and Myers 2003), and *Sibon longifrenis* specifically resembles a palm pitviper, *Bothriechis schlegelii* (photos in Greene 1997; Solórzano 2001). Rear-fanged toad-eaters in the colubrid *Waglerophis-Xenodon* clade often exhibit specific color pattern similarities to sympatric venomous pitvipers (*Bothrops*, *Bothriopsis*; Martins and Oliveira 1998; Marques et al. 2001). In Costa Rica, when threatened by a human, *X. rabdocephalus* flattens its neck and thereby enhances color pattern resemblance to *Bothrops asper* (Pough 1988a); geographic variation in Brazilian *W. merremi* encompasses apparent mimicry of sympatric *Bothrops alternatus*, *Bothrops itapeatingae*, or *Bothrops jararaca* (Sazima 1992; M. Martins, pers. comm.). *Bothriopsis bilineata* is evidently mimicked by *X. weneri* (Hoogmoed 1985; photos in Starace 1998), and the latter is presumably derived from within the *Waglerophis-Xenodon* clade (Zaher 1999). P. A. Silverstone, a student of J. M. Savage, first described the color in life of *X. weneri*: "very pretty dull blue-green, really a turquoise . . . all dorsal scales have tiny black dots" (Hoogmoed 1985, 85). *Bothriechis schlegelii* and *B. bilineata*, along with *S. longifrenis* and *X. weneri*, respectively, thus represent independent evolutionary shifts to green color patterns and arboreal habitats within clades of drab-colored, terrestrial models and mimics (Martins et al. 2001; Parkinson et al. 2002).

Behavioral head triangulation implies that species of *Dipsas* are at least abstract pitviper mimics, and inter- and intraspecific color pattern variation suggests that in some cases those colubrids mimic particular pitvipers. The widespread *D. indica* looks more like sympatric *Bothrops jararaca* in southeastern Brazil, where the two species are sympatric, than it does elsewhere in South America, and the endemic Atlantic forest *D. albifrons* even more closely re-

sembles *B. jararaca* in color pattern (Sazima 1992). Among other Neotropical colubrids, the shades-of-brown color patterns and defensive behaviors of *Pseustes poecilonotus* (juveniles only), *Tomodon*, and *Tropidodryas* also apparently mimic various *Bothrops* (Sazima 1992; Martins and Oliveira 1998; Marques et al. 2001), whereas the green color and gaping threat displays of colubrid parrot snakes (*Leptophis*) may contribute to abstract mimicry of *Bothriechis* and *Bothriopsis* (Greene 1997).

#### OLD WORLD ELAPIDS

Cobras, kraits, and other Asian elapids evidently have spawned several mimicry systems among sympatric cylindrophiids, colubrids, and each other. Contrary statements notwithstanding (e.g., Dunn 1954; Roze 1996), Asian coralsnakes (e.g., *Sinomicrurus*, Slowinski et al. 2001) and their putative mimics sometimes are ringed with red, black, and yellow or white. A kukrisnake (*Oligodon cyclurus*) at Tam Dao, Vietnam, possessed the same colorful ringed dorsal pattern as did local *S. macclellandi*; moreover, the kukrisnake thrashed erratically and bit readily when handled, as did *S. macclellandi* at that site (H. W. Greene and D. L. Hardy Sr., unpub. obs.; voucher specimens, respectively, are MVZ 224217, MVZ 224218, and MVZ 226613). Among other Asian colubrid clades, several species of wolfsnakes (*Lycodon*) look very much like sympatric kraits (*Bungarus*; Kuch 1997a; see, e.g., photos in Cox 1991), and color patterns of some reed snakes (e.g., *Calamaria lumbricoidea*, *C. schlegelii*; Lim and Lee 1989; Stuebing and Inger 1999) closely resemble those of kraits and/or long-glanded coralsnakes (two species of *Calliophis* formerly referred to as *Maticora*; Slowinski et al. 2001). *Calliophis* (= *Maticora*) *bivirgata* and *B. flaviceps* both have dark blue or black bodies with red-orange or yellow heads and tails, and thus might be Müllerian comimics as well as Batesian models for colubrids (Slowinski 1994; Kuch 1997a; photos in Manthey and Grossmann 1997). The colubrid *Ptyas mucosus* looks like and growls like the King Cobra *Ophiophagus hannah* (Young, Solomon, et al. 1999).

Among other possible Old World snake mimicry systems, some Asian keelbacks (e.g., species of *Pseudoxenodon*, Manthey and Grossmann 1997; Chan-ard et al. 1999) and other natricine colubrids flatten their necks and thus might mimic cobras (*Naja*). At Tam Dao, Vietnam, a Golden Keelback (*Rhabdophis chrysargos*) elevated its head and spread a hood when closely approached, and thereby more closely resembled the overall appearance of sympatric Chinese Cobras (*N. atra*; H. W. Greene and D. L. Hardy Sr., unpub. obs.; voucher specimens respectively MVZ 226578 to MVZ 226582 and MVZ 226617). In some parts of New Guinea the overall shape and color patterns of Viper Boas (*Candoia aspera*) are very similar to those of stout-bodied elapids (species of *Acanthophis*, O'Shea 1996).

## MIMICRY OF OTHER VENOMOUS SNAKES

In Mexico the brightly striped *Rhadinaea taeniata aemula* might be a Batesian or Müllerian mimic of sympatric *Coniophanes picevittatus* (Myers 1974), but otherwise the possibility that venomous rear-fanged species serve as models for other colubrids has rarely been considered. One Brazilian example involves *Philodryas viridissimus*, which is capable of seriously envenoming humans, and the nonvenomous *Chironius scurrulus*; *P. viridissimus* and juvenile *C. scurrulus* are brilliant green (the much larger adults of the latter are brown) and so closely resemble each other in color patterns and defensive threat displays that experienced herpetologists in the field sometimes confuse the two species (Martins and Oliveira 1998; Marques 1999). Another widespread venomous colubrid, *P. olfersii*, is bright green with a middorsal orange stripe only in southeastern Brazil, where it is sympatric with the less offensive, similarly colored, and regionally endemic *Liophis jaegeri* (Di Bernardo 1998; Hartmann 2001). Some venomous atractaspids might be Batesian and/or Müllerian mimics in that rear-fanged purple-glossed snakes (*Amblyodipsas*) often look remarkably similar to front-fanged stiletto snakes (*Atractaspis*) (photos in Spawls and Branch 1995).

*Some Unsolved Puzzles*

## INVERTEBRATES AS NOXIOUS MODELS?

Most discussions of venomous snakes and mimicry have dealt with them as putative models (e.g., acoustic defensive displays of rattlesnakes and burrowing owls, Rowe et al. 1986), perhaps on the questionable assumption that the other players, usually insects, are not noxious (reviewed in Pough 1988a). Gans (1973), however, suggested that nonvenomous shield-tailed snakes (Uropeltidae) are centipede mimics, on the basis of their similar defensive squirming behaviors and cross-barred ventral patterns, and Vitt (1992) presented compelling circumstantial evidence that some caecilians and elongate, brightly marked lizards are mimics of unpalatable millipedes and/or centipedes. Vitt (1992) also proposed that millipedes are models for coral snake mimicry, a hypothesis contradicted with field experiments by Brodie and Moore (1995). Other advanced snakes might well be millipede mimics by virtue of a tightly coiled defensive posture coupled with cross-barred ventral (*Contia tenuis*, Leonard and Stebbins 1999) or dorsal coloration (*Xenopholis scalaris*, Zug et al. 2001). Inspired by Vitt (1992), Greene (1997) suggested that because many basal snakes (e.g., *Cylindrophis*) have alternating light and dark barred ventral patterns, myriapod mimicry might have facilitated their early radiation as surface-dwelling rather than burrowing squamates. Because anguid lizards are among the near outgroups of snakes (Lee 1998b), that hypothesis is consistent with extremely sim-

ilar color patterns among millipedes and South American *Diploglossus* (Vitt 1992). Moreover, juveniles of a North American anguid with somewhat reduced limbs (*Elgaria kingi*) closely resemble sympatric large centipedes (*Scolopendra heros*) in cross-banded color pattern and sinuous locomotor escape behavior (L. J. Vitt, pers. comm.; H. W. Greene, unpub. obs.); the ventral color patterns of some species of *Diploglossus* resemble a coralsnake by having crossbars of red, yellow, and black (Savage 2002).

Several Asian land planarians look like venomous elapids in color pattern, thus potentially adding some surprising complexity to understanding venomous snake mimicry (color illustrations in Graff 1899; Fogden and Fogden 1974; Moffett 1998; photos of coralsnakes in Campbell and Lamar 1989). Among those soft-bodied invertebrates, *Bipalium everetti* of Borneo is approximately 10 cm long and has a banded dorsal body pattern of red-yellow-black-yellow-red like some Asian *Sinomicrurus*, many New World *Micrurus*, and the presumptive Old and New World colubrid mimics of those genera; *B. everetti* even has each end banded only in black and yellow, as is also typical of those elapids. *Bipalium ellioti* has a pattern of black and white bands, thus resembling some New World venomous coralsnakes (e.g., *M. mipartitus*), Old World kraits (e.g., *Bungarus multicinctus*), and putative colubrid mimics of the latter (e.g., some *Lycodon*). Another Asian land planarian, *Dolichoplana harmeri*, has black and light stripes with an orange head and tail, somewhat like an Asian long-glanded coralsnake (*Calliophis* [= *Maticora*] *bivirgata*) and its putative mimics among reedsnakes (*Calamaria*, photos in Lim and Lee 1989; Stuebing and Inger 1999).

An obvious nonadaptive explanation for the similarities between terrestrial Old World flatworms and elapids, especially Neotropical coralsnakes, is coincidence. However, ingestion of *Bipalium kewense* causes instant vomiting in cats and death in chickens, cows, and horses (Winsor 1983), and captive Bornean hornbills of two species rejected *B. everetti* as food (Fogden and Fogden 1974; M. P. Fogden, pers. comm.). Given unpalatability in terrestrial flatworms and evidence that the aposematic color pattern primitive for New World coralsnakes arose in their Asian common ancestor with *Sinomicrurus* (Slowinski et al. 2001), brightly marked planarians might even historically have been Batesian or Müllerian models for some snake mimicry systems. A third possibility is that those flatworms and venomous elapids convergently evolved particular aposematic color patterns because those combinations of hues afford the best signaling characteristics under particular light and predation threats (Hailman 1977).

#### WHY DOES MIMETIC PRECISION VARY AMONG SNAKES?

A few examples illustrate the wide range of phenotypic matching between putative models and mimics among snakes. Compared with sympatric New World

elapids (photos in Campbell and Lamar 1989; Martins and Oliveira 1998), coral-snake mimics can have similar relative band length and identical ring color order (e.g., *Micrurus hippocrepis* and *Urotheca elapoides*), similar relative band length but different ring color order (e.g., *M. fulvius* and *Lampropeltis triangulum*), different relative band length and identical ring color order (e.g., *Micruroides euryxanthus* and *Chionactis occipialis annulatus*), or different relative band length and ring color (e.g., Amazonian *Micrurus* and *Anilius scytale*). Among Brazilian colubrids that mimic *Bothrops* (photos in Marques et al. 2001), resemblance ranges from overall drab, cryptic coloration and defensive head triangulation (e.g., species of *Thamnodynastes*) to strong color pattern similarity (e.g., *Dipsas neivai* and *B. jararaca*). The green dorsums and particular markings of *Sibon longifrenis* and *Xenodon werneri*, putative mimics of *Bothriechis schlegelii* and *Bothriopsis bilineata*, respectively, also imply that specific color pattern components (rather than only abstract viper resemblance) are important in predator deception by those colubrids. Snakes thus exhibit a continuum of resemblance precision, spanning near-perfect or concrete to vaguely abstract mimicry (Pasteur 1982; Pough 1988a, 1988b). Addressing that phenomenon more generally, Edmunds (2000; see also Johnstone 2002) proposed six explanations for what he termed good and poor mimics, each of which might apply to venomous snake mimicry systems:

1. Some venomous models are more noxious than others. Clearly, within a snake fauna and given a range of predator sizes and susceptibilities, the bites of several species of sympatric elapids and viperids can vary greatly in their effects on potential predators.
2. Because of variation in sensory capabilities, what is perceived as poor mimicry by humans might be sufficient against other predators. Birds and mammalian carnivores seem particularly likely to be relevant predators in snake mimicry systems, for example, and some of the former have much more acute vision than many of the latter (Greene 1988; Martins 1996; Tanaka and Mori 2000).
3. Poor mimics might simultaneously signal palatability and danger, and thus confuse predators long enough to permit escape.
4. A poor mimic moving rapidly might be just as effective as a good stationary mimic (see Srygley 1999). The perceived image of color patterns can change when snakes move rapidly (Pough 1988a; Brodie 1992), and this explanation might even explain protective resemblance to relatively slow-moving vipers if the mimics themselves are fast moving (e.g., *Xenodon* and some other colubrids).
5. Poor mimics might be in the process of losing or evolving more precise resemblance. This hypothesis predicts local variation in color patterns, and that closely related populations will exhibit respectively better or poorer mimetic resemblance.

6. A good mimic presumably receives protection only when it is sympatric with a particular model and a relevant predator, whereas a poor mimic might receive some protection involving several models and predators over a large area.

Edmunds (2000) noted that widely foraging predators might encounter a broad spectrum of aposematic models and quickly forget the rarer ones, and that learning abilities of different predators could affect selection for good versus poor mimics. Perhaps the ease with which brightly ringed elapid color patterns versus cryptic viperid patterns are incorporated into avoidance mechanisms by predators also influences whether good or poor resemblance is favored. In any case, with respect to nonmarine, front-fanged taxa (David and Ineich 1999; total number of species in parentheses), there are approximately 46 elapids and 43 viperids in South America (89), 28 elapids and 71 viperids in mainland Asia (99), and 17 *Atractaspis*, 26 elapids, and 51 viperids in Africa (94). Global variation in the species richness and natural history of venomous putative models clearly provides many opportunities for addressing mimetic precision, and Sweet's (1985) analysis of crypsis and putative mimicry of *Crotalus* by *Pituophis* provides an exemplary methodological starting point for field studies of that problem.

#### STILL MORE QUESTIONS

Why do some colubrids (e.g., *Lystrophis dorbignyi*, Yanosky and Chani 1988) resemble vipers with their dorsal patterns and elapids with their ventral coloration (Martins 1996)? Of what significance are the bizarre "partial coralsnake" color patterns of Bornean *Bungarus flaviceps baluensis* (black and white striped anteriorly, as in the nominate race, but with red, black, and white rings posteriorly; Stuebing and Inger 1999; Kuch and Götzke 2000) and Neotropical *Scaphiodontophis* (coralsnake colors at least anteriorly, sometimes striped or unicolor posteriorly; Savage and Slowinski 1996)? A coralsnake-patterned Brazilian colubrid, *Simophis rhinostoma*, exhibits presumptive viper mimicry (tail vibration) only when threatened at night (Marques 2000), consistent with Savage and Slowinski's (1996) suggestion that species with such puzzling mosaics of defensive traits target different predators at different times and/or in different habitats.

Parallel ontogenetic and color pattern changes between models and mimics do occur (e.g., *Micrurus alleni* and *Lampropeltis triangulum* in southern Costa Rica; Savage and Vial 1974), but what factors account for great size disparity in mimicry systems, which include snake mimics that are far smaller as well as those that are much larger than sympatric models? At La Selva Biological Station, Costa Rica, for example, a geometrid moth larva less than 2 cm long is remarkably similar to sympatric *M. alleni* in color pattern, including the fact that

its anterior and posterior are bicolored whereas the body is tricolored (photos in Conniff and Murawski 2001), yet at that site the brightly ringed *L. triangulum* can be 1.5-fold longer than adults of all three sympatric species of *Micrurus* (H. W. Greene, pers. obs.). Perhaps unusually large mimics or exaggerated behavioral displays act as supernormal sign stimuli (“supermimicry”; Howard and Brodie 1973; Brodie 1976) for some predators, and tiny mimics are feasible because the size spectrum of potential prey for motmots and some other small birds (Remsen et al. 1993) encompasses neonate venomous snakes and even shorter insects.

Populations of *Erythrolamprus* vary in color pattern concordant with presence or absence of various sympatric *Micrurus* (Emsley 1966; Greene and McDiarmid 1981; Marques and Puerto 1991); *Micruroides euryxanthus* switches color pattern in sympatry with the larger *Micrurus distans* (Greene and McDiarmid 1981); and the color pattern of *Micrurus decoratus* more closely resembles that of the larger *Micrurus corallinus* than those of close relatives of the former (Marques 2002). Each of those examples implies Batesian mimicry, and granting a palatability spectrum among snakes, detailed studies of size and color-pattern shifts in sympatric South American *Micrurus* (Roze 1996) might clarify whether any venomous coralsnakes are primarily Müllerian co-mimics.

Within butterfly mimicry systems there is substantial overlap of species with similar color patterns in microhabitat and daily activity patterns (DeVries et al. 1999), and the extent to which venomous snake models and mimics overlap in space and time warrants detailed scrutiny. For seasonal activity in southeastern Brazil (Marques et al. 2000), three putative viper mimics (*Sibynomorphus neuwiedi*, *Tomodon dorsatus*, *Xenodon neuwiedii*) cluster with two species of lanceheads (*Bothrops*) and a putative coralsnake mimic (*Erythrolamprus aesculapii*); conversely, 2 other viper mimics (*Tropidodryas serra*, *T. striaticeps*) cluster with 7 nonmimetic colubrids, and all 14 of those species cluster to the exclusion of the only elapid (*Micrurus corallinus*). Perhaps raptors and other relatively large predators of those snakes (Martins 1996) are sufficiently aseasonal foragers that they encounter models and mimics regardless of seasonal activity differences in their prey.

### *Venoms and Macroevolution: The Savage-Wallace Effects*

Layla’s Paradox, the puzzle as to why competent, powerful, intelligent endothermic predators are thwarted by the defensive displays of essentially harmless ectotherms (Greene 1988, 1997), underlies the evolution of venomous snake mimicry as well as the prevalence of abstract mimicry among snakes, especially vipers. As implied by Wallace (1867) and explicated by Pough (1988a, 1988b), the solution to Layla’s Paradox is that sometimes what appears to be a harmless Costa Rican parrot snake (*Leptophis*) turns out to be an Eyelash Pitviper (*Both-*

*riechis schlegelii*), what looks like a palatable Gophersnake (*Pituophis catenifer*) is actually a Western Rattlesnake (*Crotalus viridis*), and a seemingly odd Asian lepidopteran larvae proves instead to be a juvenile Bamboo Pitviper (*Trimeresurus stejnegeri*). For many predators, much of the time, misidentification of venomous snakes as harmless could have such severe consequences that the risk of an error would be untenable.

Perhaps 25%–35% of nonvenomous snakes worldwide are mimics of elapids and/or viperids (Savage and Slowinski 1992; Greene 1997; additional species in Martins and Oliveira 1998), so a consequence of Layla's Paradox is that as dangerous models, and beyond their own diversification, venomous taxa probably have substantially contributed to overall snake diversity by protecting the lifestyles of harmless mimetic species. Without venomous viper models there likely would be no *Dasypeltis*, a clade of essentially toothless African colubrids whose egg-eating specializations are unmatched by any other snakes (Cundall and Greene 2000). And beyond simple increases in snake species richness, mimetic lineages include adaptive zones that are rare or lacking in the venomous clades themselves. Many mollusk-eating dipsadinines mimic vipers in color patterns and defensive threat displays, yet among the approximately 240 species of ecologically diverse viperids, only *Atheris* (= *Adenorhinos*) *barbouri* parallels that speciose colubrid subclade by preying on soft-bodied invertebrates (Greene 1997; Rasmussen and Howell 1998). Conversely, mimicry is taxonomically far more widespread and common among invertebrates than vertebrates, and the exceptions to that generalization likely reflect intrinsic characteristics of particular clades of organisms (Pough 1988a, 1988b). Accordingly, we summarize four macroevolutionary patterns exhibited by venomous snake mimicry as the Savage-Wallace Effects:

First, mimicry is more likely among closely related organisms that share a common body plan (e.g., among lepidopterans, among fishes; see Seigel and Adamson 1983; Pough 1988b), and thus their specific similarities (e.g., wing color patterns in butterflies) are representative of evolutionary parallelism. Mimicry is less likely among organisms that are grossly different morphologically; evidently even mimicry among major arthropod groups (e.g., salticid spiders that resemble ants; Reiskind 1976) is much less common, for example, than within Insecta. Paradoxically, crypsis often involves similarities among organisms that are taxonomically and morphologically disparate (e.g., katydids whose wings resemble leaves with herbivore damage; E. D. Brodie III, pers. comm.), and perhaps that discrepancy entails differences in the behavioral components of prey discovery (for crypsis) and prey handling (for aposematism and mimicry).

Second, mimicry spanning distantly related organisms, representative of evolutionary convergence, is more likely to involve planarians, myriapods, fishes, snakes, and other groups with relatively simple body forms. Impressive

examples are palatable larvae of tropical marine burrfish that look very much like noxious mollusks known as sea hares (Heck and Weinstein 1978), tropical lepidopteran larvae that dramatically resemble pitvipers (Pough 1988a), and legume seed pods that look like caterpillars (Lev-Yadun and Inbar 2002), whereas octopuses are spectacular exceptions to this generalization in that they mimic fish by changing color pattern and even external form (Hanlon et al. 1999).

Third, among vertebrates, snake mimicry is unusually widespread because of (1) and (2), and because venomous species can severely injure or kill predators (Wallace 1867; Pough 1988a, 1988b).

Fourth, the origin of noxious attributes can markedly increase diversity within a clade beyond that encompassed by unpalatable species; dangerous models thereby make otherwise “unprotected niches” possible for harmless relatives, and even for lifestyles not used by the models themselves. Discussions of unbalanced clade diversification typically have focused on key innovations as apomorphies for the groups in question (e.g., Hunter 1998), but the origins of noxious qualities and aposematism within snakes evidently set the scene for repeated evolution of mimetic signals that influenced overall species richness and overall clade diversity far beyond that of noxiousness per se. One way to explore that claim would be to compare sister taxa with and without mimicry against null models for symmetrical cladogenesis (e.g., Slowinski and Guyer 1993); another would be to assess proportions of species in “unprotected niches” for mainland tropical snake assemblages in which elapids and viperids are present, with roughly comparable sites on Madagascar and elsewhere that lack venomous models (cf. Cadle and Greene 1993; Cadle 2003). The latter approach would require far more detailed characterizations of snake assemblages and their predators than are now available (for important exceptions, see Martins 1996; Tanaka and Mori 2000).

### *Future Prospects*

Three general approaches offer much promise for future studies of venomous snake mimicry. First, innovative field and laboratory experiments with models (including models of vipers; Andren and Nilson 1981), detailed analyses of staged encounters with live prey (Oliveira and Santori 1999), and observational studies of free-living predators (Greene 1986) should provide complementary insights into the ethology of feeding and defense as they relate to palatability spectra (for theoretical considerations, see, e.g., Speed and Turner 1999; Rowe and Guilford 2000).

Second, we have scarcely utilized museum materials and other nontraditional approaches to study the evolutionary biology of color pattern variation. A long-standing tradition in vertebrate systematics is to summarize rather than explore variation, and few studies of snakes have assessed local and intraspecific

variation in putative models and mimics (e.g., Savage and Crother 1989; Marques and Puerto 1991). Theory predicts, for example, that Batesian models and mimics should vary within populations, whereas Müllerian co-mimics should be monomorphic (e.g., Huheey 1988; Joron and Mallet 1998), and Leenders et al. (1996) suggested that polymorphism for white or red bands within a Costa Rican population of *Micrurus mipartitus* represented attempted escape from Batesian mimics. However, a probable mimic of that coralsnake, *Urotheca euryzona*, is correspondingly dimorphic at La Selva Biological Station (H. W. Greene, unpub. obs., on MVZ 215672, MVZ 215696), approximately 20 km from their site, so that situation invites further study (see Savage and Crother 1989 for details of variation in that species). Museum specimens might also be used to explore the developmental basis for the evolution of mimicry, particularly with respect to locally variable phenotypes (e.g., Meachem and Myers 1961; Martins and Oliveira 1993, 1998; Savage and Slowinski 1996) and theoretical models for color pattern transformations in snakes (Murray and Myerscough 1991; Savage and Slowinski 1996).

Another way in which museum collections can serendipitously contribute to the study of mimicry is illustrated by observations on Scarlet Kingsnakes (*Lampropeltis triangulum elapsoides*) at Archbold Biological Station (ABS; Highlands County, FL). A preserved adult *L. t. elapsoides* (ABS 50) came from the stomach of a road-killed Great Horned Owl (*Bubo virginianus*) and thus confirms predation on this putative mimic of *Micrurus fulvius* (Greene and McDiarmid 1981). Furthermore, among 13 preserved and 1 live *L. t. elapsoides* from ABS, we recorded dorsal black ring fusion counts of 0 for 7 snakes, 1 for 3 snakes, and 2, 3, 4, and 5 for 1 snake each ( $x = 1.3$  fusions/snake). The owl's prey item has 10 ring fusions that dorsally obscure some red rings; in that sample of 14 specimens, ABS 50 is thus by far the most unlike *M. fulvius*, just as expected if the typically tricolored pattern of *L. t. elapsoides* facilitates coralsnake mimicry.

Third, aposematic and mimetic attributes that have been fixed for populations, species, and higher taxa can be studied by phylogenetic analysis (Larson and Losos 1996), and with that perspective we might better understand the historical diversification of mimicry assemblages (Turner and Mallet 1996). As Coddington (1988) pointed out, our study of geographic variation in coralsnake mimics (Greene and McDiarmid 1981) would have profited from analyses of their color pattern transformations vis-à-vis cladogenesis in elapid models, as would other snake mimicry systems (for examples with other mimicry systems, see Brower 1996; Zrzavy and Nedved 1999; Symula et al. 2001). There are as yet no detailed phylogenies for all components of any snake mimicry systems (see Wilson and McCranie 1997, regarding Smith and Chiszar 1996), but cladistic analyses are available for some of the model clades (*Bungarus*, Slowinski 1994; New World elapids, Slowinski 1995) and will undoubtedly lead to interesting insights. We know, for example, that the simple tricolored pattern that is primitive for New World elapids arose in their Asian common ancestor with *Sinomi-*

*crurus* (Slowinski et al. 2001), and therefore that bicolored and more complexly tricolored patterns are derived within a clade characterized by the former (Slowinski 1995). Among colubrids, *Lampropeltis triangulum* (Williams 1988) and *Urotheca* (Savage and Crother 1989) hold special promise for phylogenetic studies of mimetic diversification because of their extensive color pattern variation in and out of sympatry with venomous coralsnakes. The Xenodontini also has excellent potential for historical evolutionary approaches because it includes radiations of coralsnake mimics (*Erythrolamprus*) and viper mimics (*Waglerophis-Xenodon*), both within a larger clade of more generalized cryptic xenodontines (Zaher 1999; Vidal et al. 2000).

Finally, we emphasize that beginning about 135 years ago (Wallace 1867), scientific interest in venomous snake mimicry first encompassed observations from nature (some brightly marked colubrids look like deadly elapids), then indirect efforts at hypothesis testing (model-mimic ratio data); still later came controlled experiments using model snakes and only recently a preliminary theoretical synthesis. Thus far, studies of venomous snake mimicry have made only occasional contributions to our understanding of microevolutionary processes (e.g., see Mallet and Joron 1999; Rowe and Guilford 2000; Jiggins et al. 2001; Pfennig et al. 2001), but snake mimicry is proving unusually interesting in terms of macroevolutionary patterns. Our "discovery" in the natural history literature of toxic, brightly colored flatworms implies that some aspects of the "coralsnake mimic problem" still await explanation, and more generally, recent advances in phylogenetics hold much promise for unraveling the complex history of mimetic evolution in serpentine organisms. We expect that the research cycles initiated by Alfred Russel Wallace in the nineteenth century and invigorated by Jay Mathers Savage in the twentieth century will continue to occupy organismal biologists for some time to come.

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