

## EVOLUTIONARY BIOLOGY

# To mimicry and back again

**Deadly coral snakes warn predators through striking red–black banding. New data confirm that many harmless snakes have evolved to resemble coral snakes, and suggest that the evolution of this Batesian mimicry is not always a one-way street.**

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Many species that are dangerous or unpleasant to eat have evolved conspicuous signals that warn predators to avoid them. Not surprisingly, many other species that are edible to predators, from birds and butterflies to salamanders and sea slugs, have evolved to resemble these inedible species<sup>1</sup>. By doing so, the ‘mimics’ receive protection from predation, just like their ‘models’. This phenomenon is known as Batesian mimicry after the explorer and naturalist Henry Walter Bates, who first described it<sup>2</sup>. Batesian mimicry has long fascinated evolutionary biologists, and it is widely used to illustrate the power of natural selection to produce remarkable adaptation<sup>1</sup>. Yet we still do not know how common Batesian mimicry is, what its role is in evolutionary diversification, nor whether it can be reversed. Writing in *Nature Communications*, Davis Rabosky *et al.*<sup>3</sup> present findings on mimicry of coral snakes that go a long way towards answering these questions.

In 1867, the naturalist Alfred Russel Wallace

suggested that the striking resemblance between deadly coral snakes and numerous harmless species of red–black-banded (RBB) snakes reflected Batesian mimicry<sup>4</sup> (Fig. 1). However, whether coral-snake mimicry actually occurs has been questioned ever since, primarily because of the (presumed) non-concordance in the geographical distributions and abundances of coral snakes and their mimics. Several studies have attempted to address this issue<sup>5</sup>; most notably, it has been demonstrated that predators avoid artificial snakes that have RBB patterns<sup>6</sup> but only in geographical regions where coral snakes occur<sup>7</sup>, exactly as predicted by the mimicry hypothesis.

Davis Rabosky and colleagues focus on this system, but present a more comprehensive study than these earlier investigations. By integrating colour-pattern, distribution and phylogenetic data across all ‘New World’ species of snake, they show that evolutionary shifts to RBB patterns in coral snakes and numerous non-venomous species are highly correlated in space and time. Indeed, they find that every origin of the RBB pattern in non-venomous

snakes occurred only after that particular lineage and coral snakes were present together in the New World. Thus, in every case, the warning signal arose first in the model, then in the mimic, which is a key prediction of Batesian-mimicry theory. These data should therefore lay to rest any doubts about whether coral-snake mimicry does occur.

The authors’ work also shows that coral-snake diversity strongly predicts (and substantially increases) the number of mimic species in a given geographical area. Indeed, their data suggest that the ‘mimicry excess’ problem is even greater than has been historically assumed, with up to six times more mimetic than model species present in a given locality, and many more than would be expected if RBB snakes were distributed randomly across the New World. These data are at odds with the long-standing theoretical expectation that Batesian mimics should be rarer than their toxic models. However, this expectation might not apply with a highly toxic model, such as the coral snake. When the model is highly toxic, the fitness costs of mistakenly attacking it would probably be so severe that predators would be under strong selection to avoid such a model (and any lookalikes), even if the model is rare<sup>8</sup>.

Another advance that stems from this work is the authors’ proposal that mimicry might not represent an evolutionary end point. In particular, their data suggest that not only have evolutionary transitions between cryptic (non-mimetic) patterns and RBB (mimetic) patterns occurred frequently in non-venomous snakes, but so also have transitions between mimetic patterns and cryptic patterns. Most of these losses of mimicry occurred in the tropics, where coral snakes are continuously distributed,

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**Figure 1 | Protective imitation.** Many species of harmless snake, such as the false coral snake, *Erythrolamprus aesculapii* (left), have evolved the red–black-banded (RBB) colour pattern of highly venomous coral snakes, such as the Brazilian coral snake, *Micrurus brasiliensis* (right). Davis Rabosky *et al.*<sup>3</sup> show that this RBB pattern has evolved in multiple lineages of non-venomous snakes, but only after each lineage and coral snakes were present together in the New World, supporting the long-standing Batesian-mimicry hypothesis<sup>2</sup>.

suggesting that these losses occurred even among species that live in the same area as coral snakes. This is an intriguing conclusion. Generally, mimicry has been viewed as a one-way street; it is not clear why a species should ever lose mimicry once it has evolved it, particularly if their model is still around.

This suggestion will no doubt motivate further studies to determine how transitions between mimicry and cryptic patterning occur. Evolutionary biologists have long debated whether Batesian mimicry could evolve through a gradual process of incremental evolution<sup>9</sup>, and many of these arguments should apply equally to its loss. In particular, it is unclear how a population could transition from an ancestral cryptic colour pattern

to a derived mimetic one (or vice versa) if the population must pass through a phase in which it expresses a colour pattern that is intermediate between these two extremes. Such an intermediate colour pattern would be expected to be disfavoured, because it should fail to receive the fitness benefits of either cryptic patterning or mimicry.

Batesian mimicry has been called<sup>9</sup> “the greatest post-Darwinian application of Natural Selection”. Davis Rabosky and colleagues’ study has settled some questions regarding the specific example of coral-snake mimicry, and it opens the door to answering several others. ■

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1. Stevens, M. *Cheats and Deceits: How Animals and Plants Exploit and Mislead* (Oxford Univ. Press, 2016).
2. Bates, H. W. *Trans. Linn. Soc. Lond.* **23**, 495–566 (1862).
3. Davis Rabosky, A. R. et al. *Nature Commun.* **7**, 11484 (2016).
4. Wallace, A. R. *Westminster Foreign Q. Rev.* **32** (1), 1–43 (1867).
5. Greene, H. W. & McDiarmid, R. W. *Science* **213**, 1207–1212 (1981).
6. Brodie, E. D. III & Janzen, F. J. *Funct. Ecol.* **9**, 186–190 (1995).
7. Pfennig, D. W., Harcombe, W. R. & Pfennig, K. S. *Nature* **410**, 323 (2001).
8. Lindström, L., Alatalo, R. V. & Mappes, J. *Proc. R. Soc. B* **264**, 149–153 (1997).
9. Fisher, R. A. *The Genetical Theory of Natural Selection* (Clarendon, 1930).