LETTERS TO THE EDITOR

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Snake Mimicry Does Not Violate Theory

Davis Rabosky et al. (2016) report the results of a comparative study indicating that evolutionary shifts by nonvenomous New World snakes (Colubridae) to a red-black banded (RBB) coloration are correlated in space and time with the RBB pattern of venomous coral snakes (Elapidae); thus, they support the view that the former are Batesian mimics of the latter. Davis Rabosky et al. (2016: 2) state that concerns regarding this system of mimicry have arisen "because snakes clearly violate two major theoretical predictions that should hold true for mimicry to persist over long periods of time: 1) that mimics should not occur outside the geographic range of the model species; and 2) that models should be more abundant than mimics, or at least near a ratio of 1:1."

More than 50 years ago, Wickler (1965: 520) generally addressed both concerns as follows: "Poulton postulated that model and mimic should be sympatric. They need not be sympatric, however, but must only have a signal-receiver in common: a model might be in Africa and its mimic in Europe (or vice versa), functionally connected by a migratory bird. Another postulate was that mimics must be less numerous than their models. This means, correctly stated, that the receiver has to meet the mimic less often than the model, and is based on the assumption that one experience with the model has the same after-effect, the same 'weight' as has one with the mimic. This need not be so, however; in fact, the negative experience seems usually to be the stronger one." Wickler, therefore, identified the frequency with which predators encounter models and mimics and the salience of those encounters, rather than the absolute abundances of these signallers in nature, as relevant to establishing and maintaining mimicry.

Similarly, Fisher (1930: 158) stated, "Batesian mimicry by a more numerous of a less numerous form, cannot be excluded as impossible on purely theoretical grounds; for if the model were extremely noxious or the mimic a not particularly valuable source of food, the motive for avoidance may be but little diminished by the increase of the mimic. Moreover it is not so much abundance relative to the entomological collector, as abundance relative to selective agents of unknown species, and whose habits and times of feeding are therefore also unknown, which has to be considered, when this argument is used to exclude the Batesian principle." Henry Walter Bates (1862: 514) touched upon the issue of model-mimic abundances in his seminal proposal for mimicry, stating "that a mimetic species need not always be a rare one, although this is very generally the case; it may be highly prolific, or its persecution may be intermitted when the disguise

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Smithsonian Conservation Biology Institute, National Zoological Park, 1500 Remount Road, Front Royal, Virginia 22630, USA; e-mail: weldonp@si.edu is complete." Experimental studies affirm the intuition of these early contributors to mimicry, demonstrating that the size of the mimic population may depend upon the degree of aversiveness of the model (Goodale and Sneddon 1977), and that the mimic to model ratio may be high, with mimics sometimes outnumbering models (Brower 1960; Huheey 1980; Nonacs 1985).

That the preponderance of RBB colubrids examined by Davis Rabosky et al. are sympatric with coral snakes is consistent with a Batesian mimicry hypothesis, but the occurrence of mimics outside the geographic range of coral snake models does not contravene a tenet of mimicry theory. Neither is a prediction for mimicry theory violated by observations of a high relative abundance of mimics to models, whether considered with respect to the numbers of mimic and model species, as Davis Rabosky et al. did noting a "'mimetic excess' problem" in some geographic regions, or the absolute numbers of individual mimics and models present. Hence, referring to the relative abundances of models and mimics as a criterion for authenticating mimicry (e.g., Huey and Pianka 1977; Dudgeon and White 2012), or as a basis upon which to make decisions on the conservation biology of mimic and model species (Valkonen and Mappes 2014), should be approached cautiously.

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