

Butterfly mimicry rings run in circles

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Organisms face a wide variety of selective pressures that shape both the tempo and direction of their evolution, from sexual selection by potential mates or competitors to natural selection imposed by competition and abiotic factors. While rapid evolution of morphological traits can often be traced through historical and contemporary records, it remains difficult to disentangle the effect of the myriad selective pressures on trait evolution without characterizing the ecological and phylogenetic context in which they evolved. A new paper by Dipendra Basu, Vaishali Bhaumik, and Krushnamegh Kunte (1) provides unique insight into the evolutionary forces acting on critical adaptive phenotypes by comprehensively characterizing a complex but defined community of mimetic butterflies in the Western Ghats of India.

Within community assemblages, species interactions, including predator-prey interactions and intraspecific communication, are frequently mediated and facilitated

via a plethora of olfactory and visual cues. Honest warning signals that reflect prey defenses or unpalatability, for example, bright colors to warn potential predators of toxicity, are referred to as aposematic (2). Such conspicuous warning signals can quickly train predators to avoid the unpalatable species (3, 4). Distantly related, palatable species frequently evolve to resemble unpalatable species

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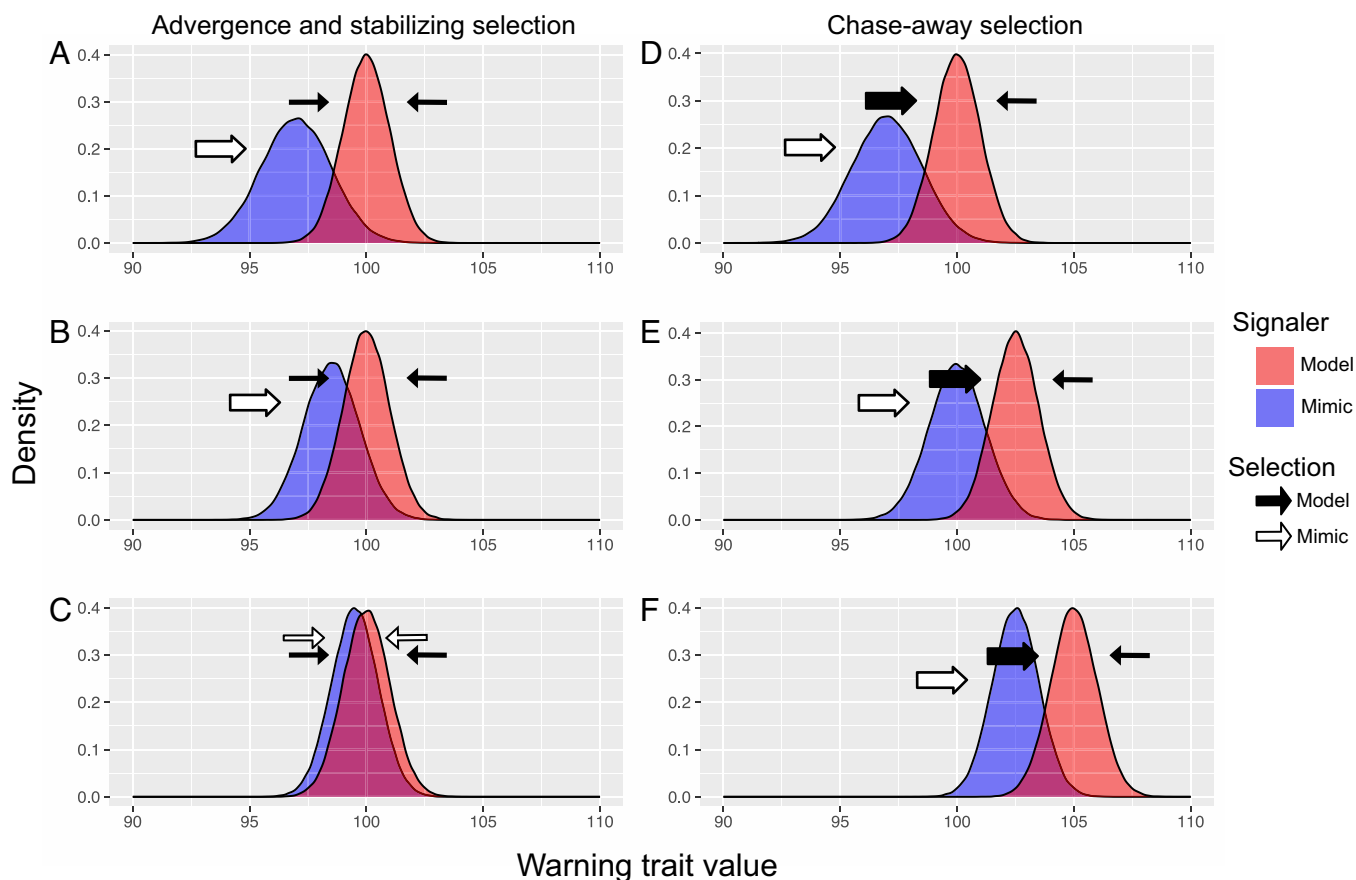


Fig. 1. Two hypotheses of mimic-model coevolutionary dynamics. Curves represent population frequencies of mimetic (blue) or aposematic (red) trait values. Arrows indicate the direction of selection, and the width corresponds to the strength of selection on each species. *Left:* The aposematic phenotype is maintained via stabilizing selection while the mimetic species experiences strong directional selection (A), and selection continues (B), until the mimetic species overlaps with the model's optimum trait value, and both are under stabilizing selection (C). *Right:* Under the chase-away selection hypothesis, as the mimic evolves toward the model under strong directional selection, the model also experiences selection to shift away from the mimic to reduce the mimetic load (D). This selection is stronger than stabilizing selection to maintain the current aposematic phenotype, resulting in a continual chase between the mimic and model (E and F).

to exploit the benefit gained from predators learning to associate aposematic phenotypes with an unpleasant experience. This form of dishonest signaling—Batesian mimicry—evolves through the process of advergence, wherein one species (the mimic) evolves to resemble an unpalatable (model) species, and therefore gains protection from predators (5, 6). Aposematism and mimicry are widespread across the tree of life with striking examples in insects, fish, birds, and mammals (7).

How do models and mimics coevolve? Our understanding of the evolutionary dynamics of Batesian mimicry has been dominated by two hypotheses. The first hypothesis posits that model species are under stabilizing selection at their phenotypic optimum (i.e., the best aposematic phenotype), while mimics are under directional selection to evolve a strong resemblance with the model [Fig. 1 A–C; (8)]. The idea that mimics evolve toward their models faster than models can evolve away from their mimics is well supported by many observations of advergence in natural mimicry systems (9) and the prediction that any deviation from an established aposematic color pattern will expose models to increased predation (8, 10).

An alternative hypothesis posits that the burden imposed on models by their mimics can lead to an evolutionary arms race or “chase-away selection” [Fig. 1 D–F; (8, 11, 12)]. Increasingly accurate mimics and a higher frequency of mimetic individuals (termed mimetic load (13)) are expected to reduce the effectiveness of aposematic cues on predator learning. This results in stronger selection on models to differentiate themselves from their mimics, the evolution of aposematic phenotypes, and reciprocal selection on the mimics to “catch-up” to their evolving models (Fig. 1 D–F; (14)). Despite theoretical support for this hypothesis, the few empirical studies investigating how models respond to mimetic load show scarce yet equivocal results on the importance of chase-away selection (15, 16).

Basu et al. comprehensively characterized mimic-model evolutionary dynamics in a defined community of butterflies localized to the tropical forests of the Western Ghats, allowing them to disentangle the effects of phylogenetic constraint and natural selection in the repeated evolution of aposematic or mimetic color patterns.

While considerable theoretical work has been done to understand the evolutionary consequences of cooccurring mimic and models, these patterns are challenging to observe in natural systems, leaving our general understanding of mimic-model evolutionary dynamics unresolved despite over 150 y of fascination with this phenomenon (17). Comparative evolution studies like that of Basu et al. (1) offer a compelling framework in which to investigate this problem. Basu et al. comprehensively characterized mimic-model evolutionary dynamics in a defined community of butterflies localized to the tropical forests of the Western Ghats, allowing them to disentangle the effects of phylogenetic constraint and natural selection in the repeated evolution of aposematic or mimetic color patterns. By comparing

phenotypic similarity between mimics and models spread across a dense, time-calibrated phylogeny, the authors identified several exciting trends in aposematic and mimetic butterfly color pattern evolution that shed light on adaptive evolution in this community.

First, the authors compared morphological traits in mimetic and nonmimetic sister taxa pairs and found that wing color patterns diverged rapidly from the ancestral background in mimics. Importantly, they did not observe these elevated rates of divergence in flight-related morphologies, suggesting that flight is more likely to be phylogenetically and functionally constrained and that focal mimicry traits appear to be specific to visual cues from wing color patterns. Next, they compared rates of evolution between models, mimics, and nonmimetic sister taxa; contrary to theoretical predictions, the authors found that aposematic color patterns and flight morphology evolved faster in the models compared to mimics. These surprising results provide compelling empirical support for the chase-away selection hypothesis and contradict the widespread expectation that mimics should evolve faster than their models, thus advancing our understanding of mimic-model coevolutionary dynamics.

The Influence of Genetic Architecture on the Rate of Adaptation

Basu et al. (1) also shed light on the role of genetic architecture on rates of adaptation in different types of Batesian mimics. Species are not always simply mimetic or nonmimetic. Sometimes they are both! In fact, several different types of mimicry may evolve, chiefly sexually monomorphic and sex-limited mimicry. Mimetic phenotypes are developed by both sexes in sexually monomorphic mimetic species, but only developed by one sex (typically females), in sex-limited mimetic species. Sex-

limited polymorphisms are widespread in nature and are thought to result from temporally or spatially varying selective pressures (see ref. 18 for a recent review). While the development and evolution of sexually monomorphic mimicry is expected to be subject to the same constraints as any other adaptive trait, recent genetic mapping studies in a variety of organisms, including the swallowtail butterfly *Papilio polytes* and its close relatives (19–21), *Papilio dardanus* (22), the nymphalid butterfly *Hypolimnys misippus* (23), *Ischnura* damselflies (24), and brown anole lizards (25) have shown that female-limited polymorphisms are frequently controlled by discrete alleles of a single switch locus. The genetic architecture of mimicry and the level of genetic constraint that mimetic phenotypes are under are therefore significantly different in sex-limited and sexually monomorphic mimics.

Switch architectures may be predicted to allow rapid, independent evolution of female and male color patterns because they alleviate genetic constraints imposed by selection on male color patterns. That is, genetic switches allow for decoupling of color patterning programs between males and females that

enable selection to independently optimize sex-specific phenotypes. Importantly, Basu et al. (1) found that female-limited mimics have evolved novel color patterns significantly faster than monomorphic mimics, providing much-needed general evidence that switch locus architectures frequently allow rapid evolution of sex-specific traits. Interestingly, the authors also showed that both genetic architectures allow mimics to evolve toward model color patterns but that female-limited mimics evolve significantly faster. While the reasons why sex-limited polymorphisms evolve, and evolve so rapidly, remain poorly characterized despite over a century of genetic investigations, studies like that of Basu et al. are beginning to lay the framework for understanding these intriguing genetic systems.

Future Directions

The results and discussion presented by Basu et al. (1) raise several interesting questions. The fast rate of aposematic trait evolution in models highlights the need for empirical studies on mimic-model chases. For example, using

well-characterized mimicry rings like those in the Western Ghats, distinct local populations of a model species can be compared to investigate whether mimetic load, and therefore chase dynamics, is correlated with the rate of evolution in the aposematic model [as done in Akcali et al. (16)]. Further, detailed pairwise comparisons of mimic-model dynamics that show differential rates of model evolution can help elucidate mimicry ring characteristics that are more likely to result in chase dynamics. Additionally, it is unclear how sensitive the observed evolutionary patterns are to the abundances and densities of model-mimic complexes within community assemblages. Previous work has drawn attention to our incomplete understanding of the ecological dynamics of mimic-model assemblages (17). Basu et al. characterized the mimetic community in a defined geographic region with a shared geological and ecological history, allowing them to control for many of those interactions. Future studies should continue to consider deeply how ecology interplays with and feeds back on the evolutionary dynamics uncovered in this study.

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