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Invited Commentary

Defensive coloration as a multivariate optimum: a comment on Postema et al

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Color is a quintessentially multifunctional trait. Although some functions are not mutually exclusive, often functions conflict. What are the main sources of conflicting selection pressures and what are the consequences for defensive coloration in animals? Postema et al. (2022) tackle these questions in their comprehensive review. They define six general scenarios that produce conflicting selection pressures on defensive coloration and propose three ways that organisms resolve these apparent conflicts—by exhibiting intermediate, simultaneous, or plastic color strategies. This provides a useful framework for understanding the evolution of defensive coloration that is applicable across the diversity of forms of defensive coloration—from crypsis and masquerade to aposematism and deimatism.

The varied solutions to conflicting selection pressures are intriguing and almost as diverse as animal color patterns themselves, but Postema et al. (2022) tentatively identify several patterns. In terms of prevalent selection conflicts, the literature is dominated by studies of multiple antagonists (conspecifics, predators, prey, parasites, and parasitoids). In terms of the three types of color strategies, simultaneous color strategies appear to be common solutions to balancing social/sexual communication needs with predator defense, whereas plastic strategies are commonly associated with ontogenetic changes and environmental variation.

To some extent, these patterns may reflect biases in the approaches used to study different color strategies or biases in the types of questions that are tractable. For example, the prevalence of studies examining selection from multiple antagonists may be due to the increasing ease and feasibility of modeling how different viewers may perceive the same color pattern (Maia et al. 2019) and modeling distance-dependent effects (Barnett and Cuthill 2014). Similarly, plastic color strategies are often studied by recording individual color responses to different stimuli or at different life stages, so it is perhaps unsurprising that they are commonly associated with environmental variation and ontogenetic changes.

Whether certain selection conflicts favor particular forms of defensive coloration or a particular color strategy remains an open question. Beyond a formal meta-analysis recommended by Postema et al. (2022), one approach to address this question is to model optimal phenotypes depending on the nature of selection conflicts. In this vein, Merilaita et al. (2008) modeled circumstances favoring intermediate crypsis in different microhabitats or improved crypsis in one microhabitat at the expense of crypsis in the other. Similarly, Speed and Ruxton (2007) developed an optimization model to predict the conspicuousness of aposematic color patterns, depending on a range of costs and benefits. There is substantial scope to develop similar models for different types of selective conflicts and different forms of defensive coloration.

Defensive coloration can be considered a multivariate phenotype, with optima on the fitness landscape defined by specific combinations of selection pressures (i.e. multivariate selection). Viewing defensive color patterns in this way opens the door to theoretical models predicting the conditions that favor particular forms of defensive coloration or color strategies. These predictions could then be tested within a comparative framework, using groups of species that vary in the selection pressures of interest. For example, in the case of conflict between aposematism and thermoregulation, one might test whether aposematic species with high contrast black and yellow or red patterns use a higher proportion of black in cooler climates (intermediate strategy).

Postema et al. (2022) make several useful recommendations for how we might empirically study multifunctional color strategies. But beyond additional empirical studies, the field would benefit from theoretical work to explicitly link selection conflicts or trade-offs to optimal color strategies. The enduring challenge for behavioral ecologists will be to move beyond the traditional approach of testing single functions of coloration to testing predicted phenotypic optima arising from multivariate selection (Cuthill et al. 2017).

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