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Digest: Strengthening the link between sexual selection and color polymorphism*

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Heritable variation is the fuel for adaptive evolution, and the processes that generate and maintain it have been the focus of intense interest since the inception of modern evolutionary biology. The level at which variation is expressed determines, in large part, the processes that maintain it. Neutral and nearly neutral molecular variation (e.g., silent nucleotide substitutions), for example, are seldom exposed to selection, and largely evolve via genetic drift (Kimura 1984). An enduring puzzle, however, is presented by extreme variation that is exposed to and persists in the face of selection.

Color patterns are conspicuous aspects of phenotypes and therefore often subject to strong selection. While some degree of within-species variation is expected for many traits, such as those involved in communication, the maintenance of discrete polymorphism raises intriguing questions that remain unanswered. Given that all individuals of a species draw upon a single gene pool, why does selection not ultimately favor a single optimal phenotype?

Extensive evidence supports a role for sexual selection in mediating polymorphism (Wellenreuther et al. 2014), though much remains to be understood about the relationship between the strength of sexual selection and the dynamics of conspicuous variation. In this issue, Pérez i de Lanuza et al. (2017) explore this question by examining whether adult sex ratios—as a measure of sexual selection—predict the richness and diversity of color morphs. They focus on the exuberantly polymorphic wall lizard *Podarcis muralis,* in which both males and females express up to five discrete color variants across their broad European distribution.

The results of the authors' survey of 116 populations reveal a striking degree of variation in both sex ratio and color-morph dynamics. They found both male-skewed and female-skewed biases of over two-to-one, and a range of color-morph richness among populations, with frequent intersexual differences in morph composition. At a broader scale, and of particular interest, the researchers identified a positive relationship between sex ratio bias and morph dynamics, though only among males. That is, male-biased populations (in which sexual selection is likely stronger) tended toward greater color-morph diversity and richness among males, but not females.

The persistence of polymorphism ultimately demands balancing selection to maintain equal morph fitness over time. Negative frequency dependence, or rare-morph advantage, is common in sexual contexts, and can be driven by intrasexual competition in which discrete coloration indicates distinct reproductive strategies. This is particularly well illustrated by the classic "rock-paper-scissors" dynamic of the side-blotched lizard *Uta stansburiana*, in which each of three male morphs enjoys a competitive advantage over only one other morph (Sinervo and Lively 1996). Drawing on a breadth of recent empirical work and their own results, Pérez i de Lanuza et al. suggest intrasexual competition may similarly contribute to male polymorphism in *P. muralis*. The cause of the apparent intersexual difference in selective pressure remains an open question, though genetic sex linkage, geographic and temporal variation in selection, and intersexual divergence in ecology are all likely contributors that remain to be examined (McLean and Stuart-Fox 2014).

Ultimately, polymorphism will be favored by a suite of adaptive and/or neutral drivers, and partitioning its causality presents an ongoing challenge (White and Kemp 2016). The opportunities offered by model systems such as *Anolis* lizards and *Papilio* butterflies have proven greatly informative, yet likely understate the causal complexity of polymorphism as it occurs more broadly. The unusually intricate morph dynamics of *P. muralis*—with interacting geographic and intersexual

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variation—offer excellent potential for unravelling enduring evolutionary puzzles around the maintenance of conspicuous variation.

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