

## Digest: Recreating ancestral trait variation to understand adaptation

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This article corresponds to Waterman, R., Sahli, H., Koelling, V. A., Karoly, K., & Conner, J. K. (2023). Strong evidence for positive and negative correlational selection revealed by recreating ancestral variation. Evolution, 77(1), 264–275. https://doi.org/10.1093/evolut/qpac001.

## **Abstract**

Two highly correlated anther traits affect pollination efficacy in a wild radish population. Does the strength and type of selection on these traits differ through male and female fitness with increased ancestral trait variation? Waterman et al. (2023) found stabilizing selection on one trait and disruptive selection on the other trait, with no difference between male and female fitness. Such quantifications of selection in populations with the increased variation that reflects ancestral trait variation provide insights into processes of trait adaptation.

Sexual selection and potential conflicts between males and females were initially studied in animals, but it is evident that the same principles are found and are important in plants, too (Willson 1979; Andersson & Iwasa, 1996). Most flowering plants are hermaphroditic and require pollinators for sexual reproduction, making it challenging to quantify selection through male and female fitness (Andersson & Iwasa, 1996). However, the quantification of selection is of key importance. Selection causes adaptation but, in the process, often reduces variation (Latta, 2010). Low trait variation in well-adapted populations, however, makes it difficult to understand the evolutionary processes that formed these traits.

In this study, Waterman et al. (2023) used populations of wild radish (*Raphanus raphanistrum*) that were artificially selected for increased variation in anther exsertion (how much the anthers protrude from the corolla tube) and anther separation (difference in the filament length between stamens with short filaments and stamens with long filaments) that resembled ancestral trait variation. By regressing the number of seeds sired and produced on trait measures, the authors quantified selection on these traits through male and female fitness, respectively.

Plants with intermediate anther exsertion had the highest fitness (indicative of stabilizing selection), and plants with either small or large anther separation had the highest fitness (indicative of disruptive selection). As there was no difference between selection through male fitness and selection through female fitness, there was no indication of sexual conflict. While intermediate anther exsertion has been shown to maximize pollen removal by small bees (Conner et al., 2009), which are the main pollinators of wild radish, the benefit of small and large anther separation remains unclear.

These results elucidate the type and strength of selection that might have been important for shaping the configuration of anther position traits observed in extant wild radish plants. They also show that, even though these traits are male flower traits, they are not necessarily under different selection through male fitness than through female fitness. More generally, they provide an empirical example of how measuring selection on increased trait variation that resembles ancestral variation may help to understand processes of adaptation. The generation of increased trait variation to study processes of trait adaptation has been used in other studies. A recent study on the functional and adaptive significance of spur length in the orchid Platanthera bifolia, for example, increased variation in flower-spur length by replacing flower spurs with plastic tubes of varying lengths that exceeded flower-spur length in the natural populations (Trunschke et al., 2020). Such an increase in trait variation is manipulative. In contrast, the approach by Waterman et al. (2023) to use plants artificially selected for increased trait variation has several advantages: All plants remain intact, variation could be increased for a wide range of traits, and differences in traits are heritable. Thus, such plants could even be used to study changes in the mean and the variation of traits over multiple generations; for example, in experimental evolution studies, such as the one by Gervasi and Schiestl (2017). This would provide more detailed and realistic insights into the processes of trait adaptation.

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