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Comment on "Evolutionary Paths Underlying Flower Color Variation in *Antirrhinum*"

Mark D. Rausher

Although Whibley *et al.* (Reports, 18 August 2006, p. 963) argue for the presence of high-fitness ridges in the *Antirrhinum* floral-color adaptive landscape, their data are equally compatible with adaptive landscapes having a single peak and no ridges. Their demonstration of divergent selection across a hybrid zone argues against the presence of adaptive ridges.

The concept of an adaptive landscape has proven useful to evolutionary biologists in understanding population divergence and speciation. Traditionally, adaptive landscapes are viewed as having multiple fitness peaks separated by low-fitness valleys (1–3). Recently, however, it has been argued that this view is likely an artifact of viewing the adaptive landscape at low dimensions and that at higher dimensions peaks are likely to be connected by high-fitness ridges along which populations can evolve by genetic drift (4, 5). If this view is correct, it suggests that genetic drift is more important in generating population divergence and speciation than is currently believed (5).

Whibley *et al.* (6) argued that their results indicate that floral colors of different *Antirrhinum* populations and species reflect a ridge of high fitness connecting a subset of possible floral-color genotypes. However, the authors appear to have overlooked another equally valid interpretation of their results that is consistent with the presence of a single peak and the absence of adaptive ridges.

Whibley *et al.* (6) tacitly assume that the adaptive landscape is identical in all populations and species. Under this assumption, one might imagine that the cloud of phenotypes in their figure 4F could correspond to a ridge in genotype space. Under this scenario, evolutionary transitions occur easily between genotypes connected by the ridge but do not occur readily through the low-fitness genotype(s) not on the ridge. However, an a priori equally likely as-

sumption is that adaptive landscapes differ among populations and species because environmental (both abiotic and biotic) conditions differ, as has been hypothesized for flower color divergence in a variety of species (7–9). Under this assumption, there is a single landscape peak in each population but the location of that peak differs among populations. Transitions between observed genotypes occur because an adapted population that experiences a permanent environmental change finds itself no longer on an adaptive peak. It therefore evolves toward a new genotype corresponding to the new position of the adaptive peak. Because at any one time and location there is a single peak, there are by definition no ridges on any of the adaptive landscapes. Nevertheless, if the positions of the locally adapted populations are plotted in genotype space, they would appear to form a cloud like that shown in figure 4F in (6). In this case, the absence of some possible genotypes (e.g., orange flowers in *Antirrhinum*) from the cloud is similar to that offered by Whibley *et al.* (6): Environments in which the landscape has a peak corresponding to those genotypes are rare.

Because the mere presence of a cloud of genotypes from different populations cannot distinguish between these two explanations, its existence cannot be taken as evidence for the presence of adaptive ridges. Moreover, additional evidence presented by Whibley *et al.* (6) argues against such ridges in the *Antirrhinum* floral-color landscape. As they state, their figure 1, B and C, indicates strong selective maintenance of steep clines involving both of the unlinked *Rosea* and *Sulf* loci, as has been demonstrated for flower-color variants in other species (10, 11).

In particular, the red *ROS/ROS SULF/SULF* genotype is favored on one side of the cline, while the *ros/ros sulf/sulf* genotype is favored on the other side of the cline. These observations indicate that introgression of alleles into one population from the other is selected against, implying that heterozygotes have lower fitness than the local homozygote. These observations thus indicate an absence of ridges connecting the homozygous genotypes, because along such ridges the heterozygote genotypes would have to have fitness equal to the homozygous genotypes [e.g., box 1 in (5)]. Instead, this pattern of selection can be most easily explained in either of two ways: (i) by differences in the position of a single peak in the adaptive landscapes on either side of the cline, or (ii) by the presence, in a single landscape that is the same on both sides of the cline, of two peaks separated by an adaptive valley involving both loci. Adaptive ridges connecting genotypes at these loci are not a feature of either explanation.

The questions of whether high-fitness ridges are a prominent feature of adaptive landscapes, and whether adaptive landscapes differ among populations, remain theoretically interesting and important. However, addressing these questions will most probably necessitate a direct quantification of adaptive landscapes themselves (e.g., 12–14), which requires accurate estimates of fitness for alternative genotypes in nature.

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