

scientific controversy distract us from attending to the needs of trauma victims (10). But criticism is vital for any scientific field, and discovering new facts, however politically incorrect they may seem, provides the best basis for helping victims. The new study's conclusion that the NVVRS overestimated the rate of PTSD by 40% will upset some people. Yet by increasing the accuracy of our prevalence estimates, Dohrenwend *et al.* have performed a valuable service. Advocacy for victims must rest on the best science possible.

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EVOLUTION

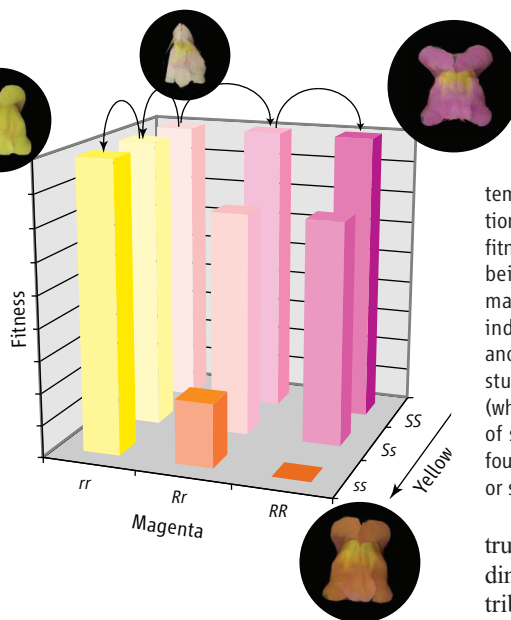
Traversing the Adaptive Landscape in Snapdragons

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How does one species become two species? Species appear to be stable, adapted entities reproductively isolated from related species, but how did this isolation appear? We can view species in terms of populations in an adaptive landscape—a topographical plot of fitness as a function of combinations of characteristics. Each species then sits on its own high ground, sporting adaptive characteristics (collectively, their phenotypes), while they tower over valleys of maladaptive phenotypes. Does this high ground represent isolated peaks, each species inhabiting one of them, or are the areas of high ground connected by an equally high ridge, long and circuitous though it may be?

Distinguishing between these two possibilities is fundamental to understanding speciation. With two isolated peaks, there is no way to get from one to the other except through great mutational leaps, tromping through a valley of low fitness, or waiting for the environment (the landscape itself) to change. In the alternative case, one can simply walk randomly along a ridge. The evolutionary mechanisms are very different between those two scenarios, including the roles of natural selection, drift, migration, and mutation. On page 963 of this issue, Whibley *et al.* provide evidence that speciation in snapdragons may have occurred through a walk along an adaptive ridge (1).

Since Wright first introduced the concept of the adaptive landscape in 1932 (2), it has



The genetic changes that underlie adaptive evolution of species are not easy to determine. Snapdragon species with different flower colors that coexist in the Pyrenees offer a promising system for analyzing them.

Evolution along an adaptive ridge. Whibley *et al.* found three loci associated with floral color, two being tightly linked and virtually inherited as one. The diagram represents their results in terms of evolution of a two-gene system along a ridge that creates reproductive isolation between the subspecies. The z axis indicates the fitness of flowers with different colors, with orange being in the valley of low fitness and yellow and magenta along the ridge of high fitness. Arrows indicate stepwise changes from one genotype to another, starting with *rrSS*. One subspecies in their study had genotype *RRSS* and the other had *rrss* (where *R* = *ROS*, *S* = *SULF*). Other extant subspecies of snapdragon are expected to contain genotypes found along the ridge but not genotypes in the valley or slopes.

become one of the most important heuristic tools in evolutionary biology. The original formulation plotted fitness in a population as a function of the frequency of different forms of specific genes (alleles), resulting in a contoured landscape where the peaks represent local optima that correspond to a particular genotype. This concept was modified by Simpson (3) and Lande (4) to yield an alternate landscape that plots fitness as a function of phenotypic values, where the surface represents the relative fitness of particular phenotypes in a population. Given that many phenotypes are quite complex at the genetic level, however, the relationship between genotype and phenotype has often proven difficult to quantify. As Wright himself pointed out, the

true adaptive landscape exists in thousands of dimensions, with many genes sometimes contributing to a single phenotype under selection. Thus, many authors have debated the true nature of an adaptive landscape: whether it is smooth or rugged, with many isolated peaks or few, with the highest level of adaptation represented by single points or by continuous ridges [see the review by Schluter (5)].

A classic model of speciation along an adaptive ridge is the Dobzhansky-Muller model. Imagine a population with individuals that have the two-locus (two-gene) genotype *rrSS* (where upper and lower case denote different alleles), and the population divides into two. In one population, a new *R* allele arises and replaces *r*, so the population now has genotype *RRSS*. In the other, a new *s* allele arises and replaces *S*, and the population has the genotype *rrss*. Note that the *R* allele has never occurred with the *s* allele during this

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process. If the combination of *R* and *s* results in low fitness, then the two new populations would be reproductively isolated (their offspring would have low fitness because they would contain both *R* and *s*), even though neither population went through any stage of low fitness itself.

Whibley *et al.* provide a possible real-world example of this process (see the figure). The authors conducted a study of naturally hybridizing subspecies of *Antirrhinum majus*, a snapdragon. The yellow-flowered *A. m. striatum* and magenta-flowered *A. m. pseudomajus* form a narrow hybrid zone where their ranges meet in the Pyrenees. Whibley *et al.* were able to identify three loci that contribute significantly to the flower color differences between the two morphs. To further investigate the evolutionary interactions of the yellow and magenta floral forms, Whibley *et al.* combined an elegant digital color quantification technique with principal components analysis to define a phenotypic space for flower color. Although the F_2 (second generation and offspring of interbred hybrids) plants from a *striatum-pseudomajus* cross occupied a relatively large portion of the space, variation observed in natural subspecies was restricted to a narrower domain. In particular, an orange-colored form obtained in the F_2 crosses was never observed in natural populations. The authors suggest that this result reflects reduced fitness due to pollinator aversion and conclude that lowered fitness among the hybrids has helped to isolate the parental genotypes. Moreover, the seemingly disjunct yellow and magenta forms are found to occupy the extremes of a contiguous domain in genetically determined phenotypic space. If the maintenance of these colors in nature reflects their higher fitness, the connection between the two extremes can be interpreted as a route for the transition from yellow to magenta while avoiding the fitness valley represented by the orange genotypes. This connection can be thought of as an adaptive ridge in which the magenta/yellow domain of genotype space represents a continuous ridge of high fitness. Populations or species tend to evolve upward toward the ridge crest, resulting in a random distribution along the ridge. In this case, it appears that one defining feature of the ridge is that when two populations come into contact, their hybridization produces some phenotypes that “fall off” the ridge, resulting in lower fitness.

The current study is possible because the authors can make accurate predictions about the relationships between color and genotype, allowing the conversion between phe-

notypic and genotypic space. The genetic simplicity of the system makes it irresistible for actual tests of the Dobzhansky-Muller dynamic through measures of natural selection on the different genotypes. Note that an adaptive landscape describes the relationship between genotypes and fitness in a single environment. The model therefore would make the simple and testable prediction that all extant floral color genotype combinations would have comparable fitness across the entire geographical range of distribution, and all missing phenotypes (presumably those carrying the incompatible combination of *R* and *s*) would have equally low fitness across the range. The alternative hypothesis is that each color morph is locally adapted to its own local environment. Such measurements would address a fundamental question regard-

ing speciation, namely whether environment-independent genetic incompatibilities alone account for reproductive isolation between species that have diverged essentially through drift along a ridge, or whether divergent adaptation to different environments is the cause. In short, just what is the role of natural selection in speciation?

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ASTRONOMY

A Journey Through Time

Joseph Silk

Small variations in the temperature and density of matter just after the Big Bang are thought to have been the seeds for the galaxies we see today. This picture has been confirmed by observational evidence.

The cosmic microwave background radiation left over from the Big Bang provides a unique window on the very early universe. We believe now that galaxies formed as small variations in matter density evolved under the influence of gravity. If so, then the primordial fluctuations had to have a finite amplitude given the limited time available for fluctuation growth. An inevitable consequence is that temperature fluctuations must be generated in the cosmic microwave background. Recent observations of the background radiation confirm this picture of the gravity-induced growth of structure in the early universe.

The first predictions of cosmic temperature fluctuations were made in 1967 by Sachs and Wolfe (1). It was not until 1992 that NASA's Cosmic Background Explorer (COBE) verified, to within a factor of 2, the predicted effect (2). This is with hindsight also the prediction of the inflationary theory of cosmology of large-angular scale temperature fluctua-

tions generated in the first 10^{-36} s of the Big Bang. It was to take more than a decade, however, before the fine-scale anisotropy predictions (3, 4) associated with galaxy formation were confirmed (5).

Each time there was a major experimental improvement, the theoretical hurdle was raised as the predictions were refined. The ultimate prediction of temperature fluctuations arising from structure formation, made in 1984 (6, 7), was only 3 parts in 100,000, at an angular scale of about 30 arc min, and substantially lower on smaller angular scales. Eventually, ground-based and balloon-borne experiments provided strong confirmation of the elusive signal. But it was the release of first-year data from the Wilkinson Microwave Anisotropy Probe (WMAP) satellite in 2003 that provided the first high-precision measurements (8). Cosmology would never be the same again with the new refined measurements.

There were several dramatic results. The universe had to be flat, and at the critical density. Most of its mass-energy density was in the form of dark energy. One-third of the critical density was in nonbaryonic matter, and only 15% of that was in baryons (such as neutrons and protons). The primordial fluctua-

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