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Evolution: Plasticity versus Selection, or Plasticity and Selection?

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Whether phenotypic plasticity enables or hinders genetic adaptation has been debated for over a century. A study of lizard coloration uncovers the means by which plasticity can facilitate colonization of novel environments and enable eventual adaptation by natural selection.

Natural selection acts on phenotypes, yet evolution occurs at the level of genotypes. Accordingly, the more direct the links are between phenotypes and genotypes, the more effectively natural selection can shape genetic variation and drive adaptation. The ability of organisms to modify their phenotypes in response to environmental conditions — referred to as phenotypic plasticity — is often thought to reduce the efficacy of selection by disrupting the associations between phenotypes and genotypes [1]. This suggests that plasticity may largely impede adaptive evolution. However, it has been posited that plasticity may facilitate or even promote adaptation in certain contexts. This debate over the relationship between plasticity and selection has continued for the last century. For example, Baldwin hypothesized in 1896 that plasticity enables populations to persist in novel environmental conditions, and that over time natural selection will 'fine-tune' the population to the environment by modifying the range or average phenotype of the plastic response [2–4]. A more recently proposed 'plasticity-first' hypothesis suggests that standing variation in plasticity itself may be exposed to selection upon colonization of a new environment, thus allowing for adaptive evolution of the plastic response [5–7]. The lack of robust empirical evidence from natural systems has, however, prevented the wide acceptance of these and other similar hypotheses, prolonging the longstanding debate about the role of plasticity in adaptive evolution [1,5,7–10]. A new study by Ammon Corl and colleagues [11] in this issue of *Current Biology* presents important empirical evidence for the synergistic roles of plasticity and adaptation in the successful colonization of a new environment by side-blotched lizards (*Uta stansburiana*).
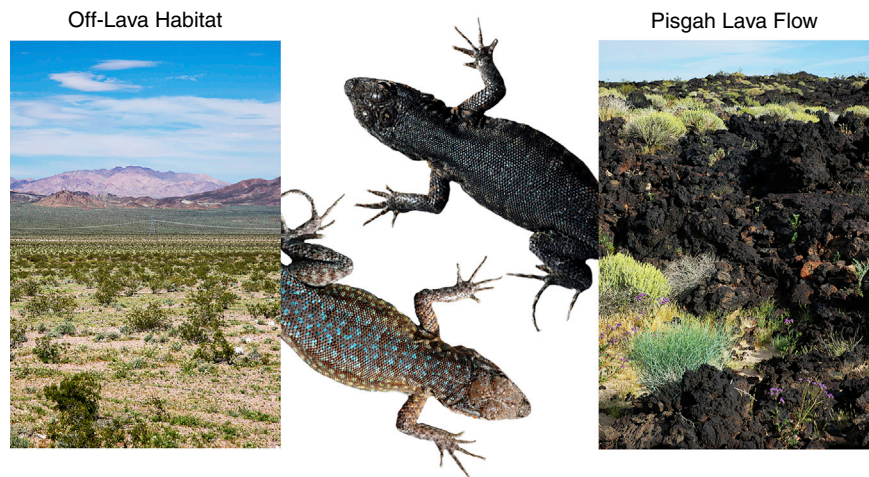
Side-blotched lizards that inhabit the Pisgah Lava Flow in southern California exhibit a dark, melanistic coloration that facilitates crypsis on dark volcanic rocks. This dark phenotype is distinct from other nearby lizard populations that live on lighter-colored soil and are more lightly colored (Figure 1). The coloration of both lava and off-lava populations is phenotypically plastic, however, such that lava flow lizards housed on light soil develop a significantly lighter coloration while off-lava lizards housed on darker volcanic rock develop a significantly darker coloration. Interestingly, lizards from the Pisgah Lava Flow population are capable of achieving a darker coloration than off-lava lizards housed

on the same dark, volcanic substrate. Thus, despite substantial plasticity of coloration in both populations, the darker melanistic coloration of lava flow lizards appeared to have a genetic component, and thus was likely to be the result of adaptation to a novel, darker environment.

To test for a genetic basis of dark coloration and investigate the roles of plasticity and adaptation in the establishment of Pisgah Lava Flow lizards, Corl and colleagues [11] first surveyed genomic variation from exome-capture data and quantified genetic differentiation between the Pisgah Lava Flow and nearby off-lava populations. The lava and off-lava populations showed remarkably low genetic differentiation from one another, suggesting minimal divergence between populations. Several genes, however, were highly differentiated between the populations on and off the lava flow, including two genes known to influence coloration. The first gene, prolyl endopeptidase (*PREP*), regulates the production of the pigment melanin [12], and the second, protein kinase cAMP-dependent type I regulatory subunit alpha (*PRKAR1A*), is associated with hyperpigmentation in humans [13,14]. Notably, the single-nucleotide polymorphisms (SNPs) underlying high differentiation in these two genes were present in the Pisgah Lava Flow population, but were not found in the focal off-lava population or nine other adjacent populations. Simulations suggested that these derived alleles arose recently, long after the initial colonization of the Pisgah Lava Flow, and were likely subject to strong positive selection in the lava flow population.

The association between these two genes and dark coloration was verified by studying a recently hatched cohort of lizards raised in a common environment. Individuals that possessed the Pisgah-specific derived alleles for at least one of these two genes were significantly darker in color than those with only the ancestral, off-lava alleles. Thus, the additive effects of these derived alleles are likely to have expanded the phenotypic range of color plasticity in the lava flow population, allowing these lizards to achieve a darker, more melanistic coloration that increased their fitness in the darkly-colored Pisgah Lava Flow environment.

Off-Lava Habitat   Pisgah Lava Flow

Current Biology

Figure 1. Side-blotched lizards from the Pisgah Lava Flow.
Plasticity in coloration of side-blotched lizards enabled colonization of the Pisgah Lava Flow and persistence long enough for new mutations to arise and be positively selected, leading to even darker coloration in this population. Images: Bob Wick and Ammon Corl.

Collectively, the results of Corl and colleagues [11] suggest an intriguing narrative for the interaction between plasticity and adaptation that allowed for the establishment and persistence of side-blotched lizards in the dark environment of the Pisgah Lava Flow. Given that current lava and off-lava populations both exhibit plasticity in coloration, plasticity is likely to have evolved prior to the colonization of the Pisgah Lava Flow. When lizards initially colonized the lava flow, phenotypic plasticity may have permitted a degree of background matching that was sufficient to enable survival and persistence in this novel darker environment. Over time, genetic changes occurred in the Pisgah Lava Flow population that shifted coloration towards the induced plastic response, allowing for even darker coloration and better crypsis. These genetic changes subsequently rose in frequency in the lava population through positive selection, as darker lizards would represent less conspicuous targets for predators and accordingly would be more likely to survive and reproduce, thus passing the genetic changes underlying darker phenotype on to their offspring. Plasticity therefore facilitated initial colonization and survival of the population in a novel environment and allowed time for subsequent genetic adaptation to 'fine-tune' the plastic response to this environment. This

interplay between plasticity and adaptation as theorized by Baldwin in 1896 has been demonstrated in multiple systems, although often with little to no understanding of the genetic basis for the traits of interest [5,7,15]. In this study, Corl and colleagues [11] provide one of the most detailed and empirically-supported examples of the 'Baldwin effect' to date by identifying and validating the role of PREP and PRKAR1A in facilitating darker coloration in the Pisgah Lava Flow population. These specific genes will likely serve as valuable candidate genes for understanding adaptive changes to coloration in other natural systems, especially in cases where selection has acted on a plastic coloration phenotype.

Perhaps the most important contribution of this study is the identification of the specific process by which plasticity facilitated adaptive evolution of melanistic coloration in the Pisgah Lava Flow. While some aspects of the 'plasticity-first' hypothesis are supported, for example that plasticity can precede and potentially promote adaptive evolution, the means by which adaptive evolution occurred in the Pisgah Lava Flow population is distinct from the specific expectations of this hypothesis. The 'plasticity-first' hypothesis suggests that previously masked variation in plastic responses

can be exposed following the colonization of a new environment in which different induced phenotypes are beneficial, thereby exposing this variation to selection and facilitating adaptive evolution [5–7]. In this study, however, the derived selected variants identified in *PREP* and *PRKAR1A* were not found in any nearby lizard populations, and simulations support the hypothesis that these alleles arose recently within the Pisgah population. This instead suggests that adaptation to the dark substrate of the Pisgah Lava Flow occurred through selection on novel mutations that arose in the Pisgah population after it colonized the lava flow, rather than through selection on standing variation present before colonization. Thus, in this example plasticity allowed sufficiently long survival of the Lava Flow population for novel beneficial mutations to appear, which were subsequently subject to natural selection. The findings of Corl and colleagues [11] provide an extended and empirically derived view of the role of plasticity in facilitating adaptive evolution beyond the expectations of the 'plasticity-first' hypothesis, such that plasticity can permit the evolution of novel genotypes and phenotypes and facilitate eventual adaptation to new

environments, even in the absence of relevant standing variation at the time of colonization.

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Neuroscience: Intracranial Recordings of Value

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The role of orbitofrontal cortex in value-based choice is well-established from animal research, but there are challenges in relating neurophysiological recordings from animals to equivalent data from humans: a new study bridges this gap.

In daily life we are constantly making decisions: what to wear, what to have for lunch, where to go on holiday in summer. In order to make choices between multiple alternatives, the brain somehow needs to compare them using a 'common currency'. One hypothesis is

that the brain facilitates this by computing a single value for each alternative by considering multiple sources of evidence indicating how good the option is. For example, if you wanted to decide whether or not to watch a particular movie tonight, you

may consider how good the trailer is, whether your friends liked it or not, whether it has good reviews, and your previous experiences with movies of the same genre. All these factors are summarized in a single value, enabling us to easily compare completely