Evolution and the Flexible Organism

Do environmentally induced changes to individuals affect natural selection, and if so, how?

David W. Pfennig

Genes are often thought to solely dictate an organism's features. Yet, naturalists have long realized that an organism's environment can profoundly shape its attributes. Take three examples. First, on a riverside beach, a female red-eared slider turtle deposits her eggs in a shady, cool location. Nearby, another female lays her eggs in a sunny, warm spot. When the eggs hatch, the turtles from the cool nest are males, whereas those from the warm nest are females. Second, in a desert pool, a family of Mexican spadefoot toad tadpoles grazes on plankton and algae. One of them encounters a school of fairy shrimp and eats some. Within days, this individual is transformed from a gregarious, slow-moving omnivore with a narrow head (like its siblings) into a solitary, rapidly swimming carnivore with a broad head. Finally, in an open field, a wild radish plant is attacked by cabbage white butterfly caterpillars. Within hours, the plant dramatically increases the production of defense chemicals in its leaves, which deters further attacks by caterpillars. In each of these three examples, an organism's environment—specifically, the temperature it experiences, the food it eats, and the predators it encounters—alters its features; that is, its *phenotype*.

In other words, each is an example of *phenotypic plasticity*, or simply *plasticity*. Such developmental flexibility has attracted considerable attention in recent years because it illustrates how environmental conditions can influence an organism's features, sometimes dramatically so. Indeed, new research has revealed that nearly all organismal features emerge from the interplay of genes and environmental factors; that, under certain circumstances, some environmentally modified traits can be passed on to offspring; and that phenotypic plasticity might jump-start and alter the course of evolution for a given species. In some cases, plasticity might have left an indelible imprint on the history of life.

David Pfennig

Spadefoot toads produce shape-shifting tadpoles that are models for studying phenotypic plasticity.

As it turns out, explaining why the members of a single species typically vary in their traits is an enduring problem in biology. For instance, the first two chapters of Charles Darwin's *On the Origin of Species* focus exclusively on the causes of trait variability. To Darwin, explaining trait variability was crucial. He understood that variation—together with inheritance and differential reproductive success—is a prerequisite for evolution by natural selection, the process responsible for the exquisitely adapted features that characterize living things. Nevertheless, Darwin struggled to explain how trait variability arises to the end of his life in 1882, when in his final year he wrote, "There is hardly any question in biology of more importance than this of the nature and cause of variability."

Ironically, nearly two decades before Darwin wrote these words, an obscure Moravian monk had published a short paper that would ultimately form the basis for what is now widely accepted as the cause of trait variability. In this paper, Gregor Mendel showed that parents transmit to the next generation discrete but invisible particles that predictably influence the traits of their offspring. However, Mendel's paper was ignored until it was discovered in 1900 when, in the span of only three months, three different scientists independently published studies that recapitulated Mendel's earlier work. Shortly after that, the Danish biologist Wilhelm Johannsen gave a name to Mendel's particles: genes. Following this rediscovery of Mendel's work, a gene-focused perspective characterized the *evolutionary synthesis*, the melding in the 1930s and 1940s of Darwin's ideas with the emerging field of genetics. Today, genes are widely viewed as the difference-makers in determining what traits an organism produces; by contrast, the influence of

QUICK TAKE

Phenotypic plasticity—in which organisms produce different features in different environments—is ubiquitous, but whether and how it impacts evolution is not fully understood.

Contrary to longstanding ideas, phenotypic plasticity may play a crucial role in facilitating evolution by promoting population persistence and exposing hidden genetic variation.

Knowledge of plasticity enhances our understanding of the role the environment plays in evolution by both selecting phenotypic variation and helping to generate that variation.

David Pfennig

Spadefoot toads breed in ephemeral, rain-filled pools in North American deserts. Their tadpoles are born as an oval-shaped omnivore morph (*on the left in inset*). However, if a young tadpole eats meat, it may develop into a distinctive carnivore morph (*on the right*). Research on such phenotypic plasticity is now revealing its role in evolution.

the environment on trait production is often ignored.

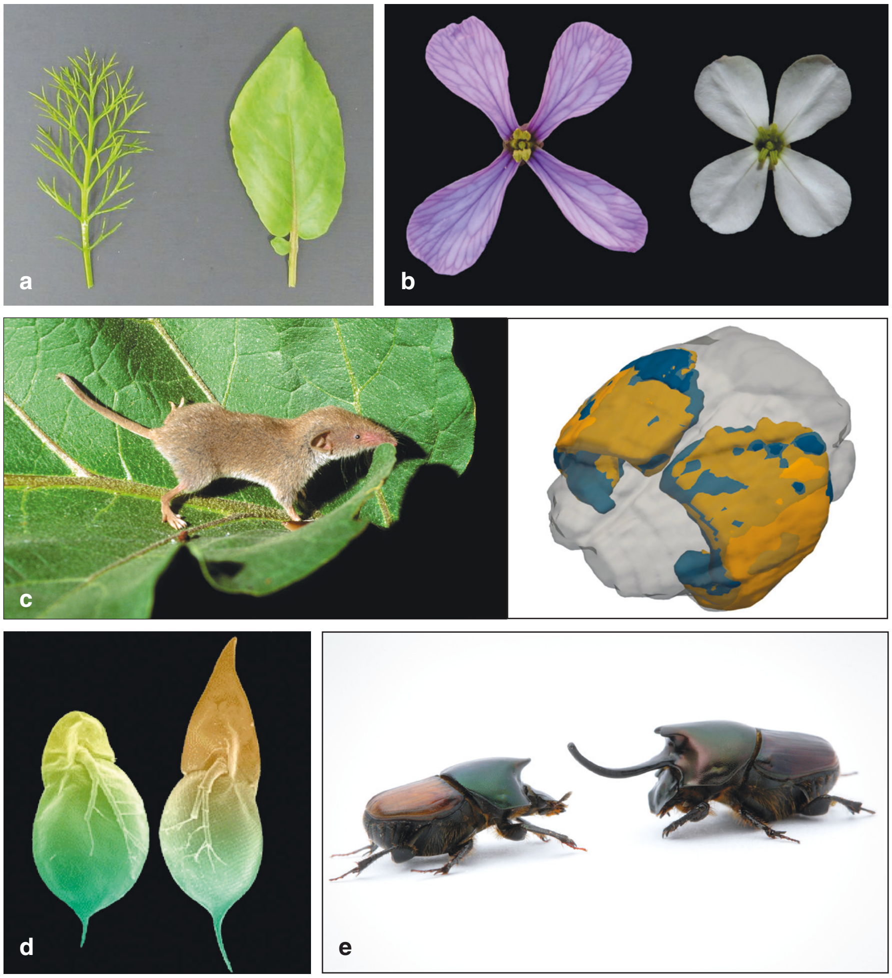
However, as we saw in our three opening examples, genes alone do not determine an individual's features. Indeed, when coining the term *gene*, Johannsen also introduced the concepts of *genotype* to refer to an organism's genetic makeup and *phenotype* to refer to its observable characteristics (that is, its morphology, physiology, and behavior). In doing so, he stressed that the phenotype results from an interplay between genes and the environment. Around the same time, the Swedish biologist Herman Nilsson-Ehle coined the term *phenotypic plasticity*, which is now defined as the ability of an individual organism (or a single genotype) to produce multiple phenotypes in response to different environmental circumstances.

But how does plasticity fit into modern biology, which often treats phenotypes as products of genotypes? This question has motivated the research in my lab for the past three decades, focusing primarily on the aforementioned shape-shifting spadefoot toad tadpoles. Our research and that of many other scientists point to an inescapable conclusion: Plasticity might play a crucial role in promoting evolution. Indeed, integrating plasticity into modern evolutionary theory may help explain a wide range of phenomena, from how novel, complex features arise to how plants and animals can persist in the face of rapid environmental change. But before addressing these issues, we need to discuss why plasticity is ubiquitous and why it evolves.

Plasticity Is Ubiquitous

We now know that all major groups of organisms, from bacteria to mammals, can react to variation in their external environment by undergoing reversible or irreversible changes in some aspect of their phenotype. These changes can be conspicuous, as with the turtles and tadpoles. Often, however, these changes occur solely at the molecular level and might not be apparent to an observer. For instance, research in just the past decade has demonstrated that diverse environmental conditions, such as temperature and diet, can influence whether individual genes are active and how much protein or RNA they make when they are active (RNA, like DNA, is a nucleic acid found in all cells; its principal role is to carry instructions from DNA for making proteins, but it can also regulate the expression of other genes). Such environmentally induced change in gene expression enables organisms to produce the appropriate proteins for current circumstances. This observation—that gene activity is environmentally sensitive in all living things—suggests that plasticity is ubiquitous.

A key to understanding why plasticity is ubiquitous is to appreciate that it is often beneficial. Of course, some



The plant *Rorippa aquatica* (*a*) produces different leaves below (*left*) and above (*right*) water. Changes in temperature and day length cause *Moricandia arvensis* to produce different flowers (*b*). To use less energy in winter, shrews (*c, left*) decrease brain size (*c, right*). The cortex of the same shrew in winter (*blue*) changes in summer (*orange*). Water fleas (*d*) produce normal (*left*) or, around predators, helmeted forms (*right*). Early nutrition determines whether male dung beetles grow horns (*e*). Rock ptarmigan change skin color seasonally (*f*).

instances of plasticity likely represent an unavoidable consequence of fundamental laws of chemistry or physics and are therefore not necessarily beneficial. For instance, poor nutrition leads to stunted growth in most organisms. Yet, many forms of plasticity do increase an individual's evolutionary fitness. For example, recall the aforementioned predator-induced plasticity in wild radish plants. But how does the fact that plasticity can be beneficial explain its ubiquity?

To answer this question, consider that every natural environment varies, whether in time or space, and due to physical or biological factors. Moreover, individual organisms often encounter environmental variation within their lifetimes, such as when an organism experiences different seasons or migrates across different habitats. This environmental variation is generally harmful; it erodes the match between the organism's phenotype and its environment. Although evolution by natural selection can help maintain this match, evolution can only occur between generations. Consequently, adaptive evolution is always at least one generation behind in responding to a rapidly changing environment. By contrast, plasticity creates phenotypic change within generations and can therefore potentially keep up with rapid environmental change. Presumably, this unique evolutionary advantage explains why plasticity is ubiquitous.

Evolution of Plasticity

Not all species nor all traits within species show similar levels of plasticity. Some features in some species are easily modified by the environment (that is, they show high levels of plasticity), whereas others are not (that is, they show low levels of plasticity). Moreover, plasticity can be expressed as either continuous or discrete variation. What conditions favor high versus low levels of plasticity, and, once plasticity does evolve, what determines its form?

Evolutionary theorists, such as Samuel Scheiner of the U.S. National Science Foundation, have developed mathematical models predicting that higher levels of plasticity (more precisely, greater environmental influence on the production of a particular trait) will evolve when the following conditions are met: 1) the benefits of expressing plasticity outweigh its costs; 2) genetic variation for plasticity is present; 3) the organism experiences environmental variation; 4) no fixed trait does best across all environmental circumstances that an individual might face; and 5) individuals can assess their environment reliably.

To determine if these conditions are met in species that have evolved high levels of plasticity, we begin with the first two conditions above (1 and 2). Decades of research have searched for costs of plasticity, and such studies have generally failed to document significant costs. Thus, the benefits of expressing plasticity likely often outweigh its costs (condition 1). Also, biologists have known since the pioneering work of ecologist Anthony Bradshaw in the 1960s that different genotypes typically vary in whether and how they respond to any particular environmental cue. Thus, genetic variation for plasticity is usually present (condition 2).

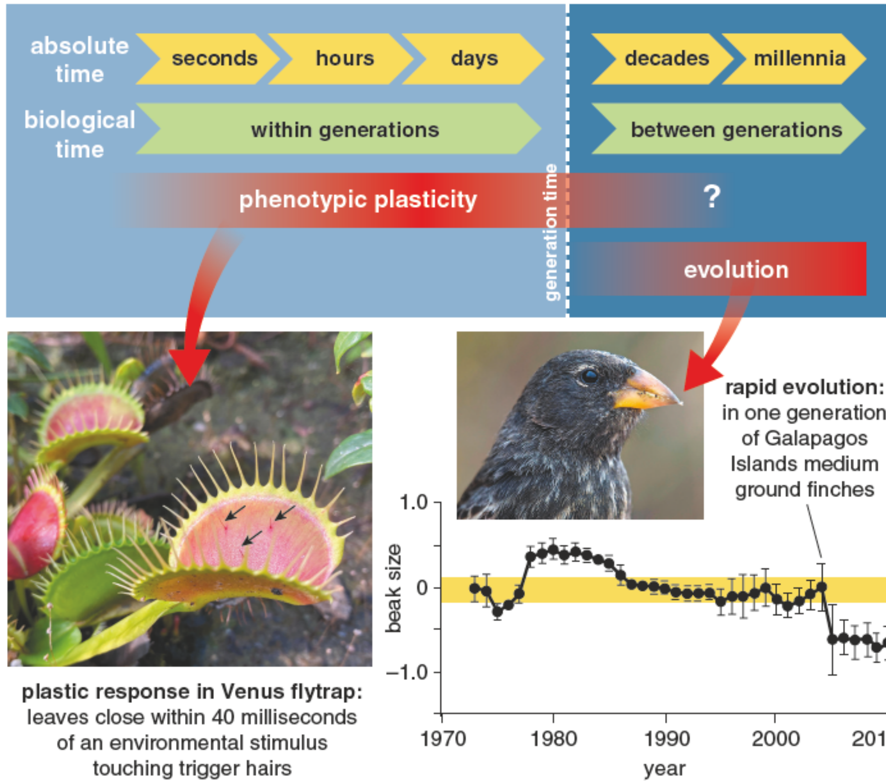
To illustrate how to test the remaining three conditions (3, 4, and 5), consider environmental sex determination, a common form of plasticity in which the environment that an individual develops in determines its sex (temperature-dependent sex determination, as in the turtles in the opening paragraph, is a particular case). Applying the theory above, sex should be environmentally influenced if individuals experience environmental variation (condition 3); the environment in which an individual develops has different fitness consequences for

Nakayama H., et al. 2014. *The Plant Cell* doi:10.1105/tpc.114.130229; Gómez J.M., et al. 2020. *Nature Communications* doi:10.1038/s41467-020-17875-1; WILDLIFE GmbH/Alamy Stock Photo; Ray S., et al. 2020. *Proceedings of the National Academy of Sciences of the U.S.A.* doi:10.1073/pnas.1922888117; Courtesy of Ralph Tollrian; ©Alex Wild; Jan Frode Haugseth/Wikipedia Commons males versus females (condition 4); and individuals can assess their environment reliably during development (condition 5).

Support for these predictions comes from studies of diverse species. One such study involves the amphipod crustacean *Gammarus duebeni*, which occurs in temperate coastal marshes. In this species, sex is determined by photoperiod, or day length, with males being produced early in the mating season, when day length is shorter, and females later, when day length is longer. Being produced early in the mating season allows males more time to grow, and male fitness improves more than female fitness with size. Thus, because males benefit from larger size more than females, and because individuals can assess their environment, environmental sex determination is adaptive in this system, presumably explaining why such plasticity has evolved.

Once increased plasticity has evolved, it can produce phenotypes that are distributed continuously or discontinuously. Continuous plasticity is more common and can allow individuals to finely tune their phenotypic response to the strength of an environmental stimulus. For instance, in the presence of predators, tadpoles of many frog species develop deeper tails, which enhances survival. Moreover, the greater the risk of predation, the deeper the tadpole's tail. Discontinuous plasticity is referred to as *polyphenism*. Examples include environmentally influenced sexes, castes in social insects, seasonal forms, predator-induced forms, and alternative resource-use and reproductive forms found in many organisms. Generally, polyphenism is thought to evolve from continuously varying plasticity when selection favors distinct phenotypes adapted to specific ecological circumstances.

However, not only can selection enhance plasticity, it can also reduce it. In particular, selection can cause a trait to evolve to become *less* responsive to a specific change in the environment, in some cases even to the point of eliminating the plasticity. Generally, selection might favor the loss of plasticity when any of the five conditions favoring an increase in plasticity outlined earlier in this section no longer hold. When selection causes a plastic trait to evolve to become fixed, the trait is said



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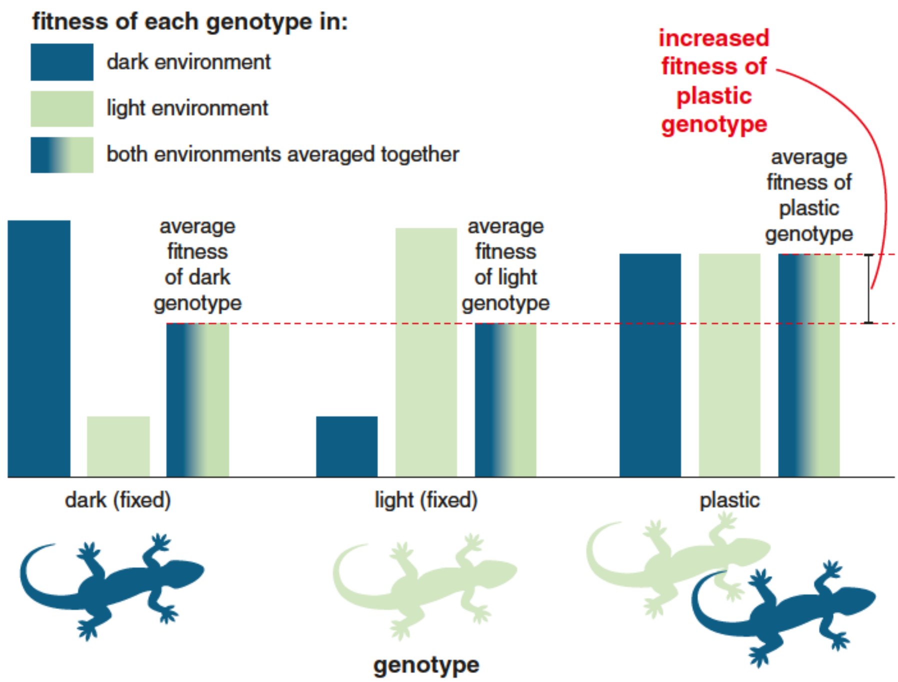
Plasticity enables organisms to respond to environmental change within a generation. By contrast, with evolution, organisms can only respond to such environmental changes between generations; even rapid evolution takes at least one generation. Sometimes, phenotypic changes wrought by plasticity can be transmitted between generations.

to have undergone *genetic assimilation*. Genetic assimilation was first demonstrated in the 1950s through groundbreaking lab experiments by geneticist Conrad Waddington. Recent research has uncovered numerous possible examples from natural populations such as my work involving spadefoot toad tadpoles. Thus, plasticity can evolve. This evidence raises the issue of whether plasticity's evolution can, in turn, affect evolution.

Plasticity creates phenotypic change within generations and can therefore potentially keep up with rapid environmental change.

Does Plasticity Affect Evolution?

Evolutionary biologists have long grappled with understanding how plasticity affects evolution. To the degree that plasticity was thought to matter, it was generally believed by many evolutionary biologists to impede evolution. After all, if a single genotype can produce multiple phenotypes in response to different environmental circumstances, further genetic change might not be required to adapt to new circumstances. In such situations, plasticity should dampen diversifying selection and impede evolution. However, rather than preventing evolution, others have hypothesized that plasticity might make evolution *more* likely to occur. For example, the distinguished evolutionary biologist Mary Jane West-Eberhard of the Smithsonian Tropical Research Institute has argued that "most phenotypic evolution begins with environmentally



David Pfennig/adapted by Barbara Aulicino

Phenotypic plasticity enhances evolutionary fitness in a variable world. Although individuals with fixed phenotypes might have higher fitness than those with plastic phenotypes in an environment for which they are specialized (such as a dark lizard in a dark environment), plastic individuals will have higher fitness when averaged across environments. Because organisms typically experience multiple environments in their lifetimes, this gives an overall fitness advantage to plastic individuals.

initiated phenotypic change. Genes are followers, not necessarily leaders, in phenotypic evolution." Here, I discuss two non-mutually exclusive ways by which plasticity might facilitate evolution. As I also emphasize below, these ideas are currently the subject of considerable research.

First, plasticity might facilitate evolution by promoting population persistence. Because plasticity can enhance individual fitness in rapidly changing environments, it should also prevent populations under stress from going extinct. Consistent with this premise, a recent study found that bird species that exhibit higher levels of plasticity (as measured by a higher propensity to innovate behaviorally) are at a lower risk of extinction than species that display lower levels of plasticity. If plasticity promotes population persistence, it could buy time until a population acquires new genetic variants—for example, by mating with members of another population or even another species—that enable it to adapt to a new environment. Because lineages that remain viable can continue to evolve and even diversify, any process, such as plasticity, that decreases extinction risk should thereby foster evolution.

Although most evolutionary biologists and ecologists probably view this *buying time hypothesis* as the primary way plasticity promotes evolution, more direct tests of the hypothesis are needed. A way to do so would be to conduct experiments using different populations that vary in degree of plasticity. One could then ask if, in the presence of a novel environment, more plastic populations are more likely to persist because of their higher levels of plasticity.

Second, plasticity might facilitate evolution through *plasticity-led evolution*. To understand how this process works, consider that most natural populations contain abundant genetic variation that is normally not even expressed, meaning that it has no effect on an organism's phenotype. However, this "cryptic" genetic variation can be expressed phenotypically when populations experience novel or stressful conditions, such as environmental changes. The phenotypic expression of this variation is crucial because selection acts on phenotypes, not genotypes. Yet, selection can only act on phenotypes that are expressed, such as those induced by the environment. Once phenotypic variation is present, selection can act on it and favor those phenotypes—and their underlying genotypes—that are well adapted to the new environment. As long as the environment persists, selection can refine the environmentally induced phenotype.

Moreover, depending on whether or not plasticity continues to be favored, selection can also respectively promote either increased environmental sensitivity—leading to a polyphenism—or decreased environmental sensitivity—leading to genetic assimilation. Either way, plasticity-led evolution produces a new phenotype that was not present in the ancestral population, at least not in a well-adapted form. Thus, in contrast with mutation-led evolution, in which a new phenotype first appears following a change in the genome, with plasticity-led evolution, a new phenotype first appears following a change in the environment.

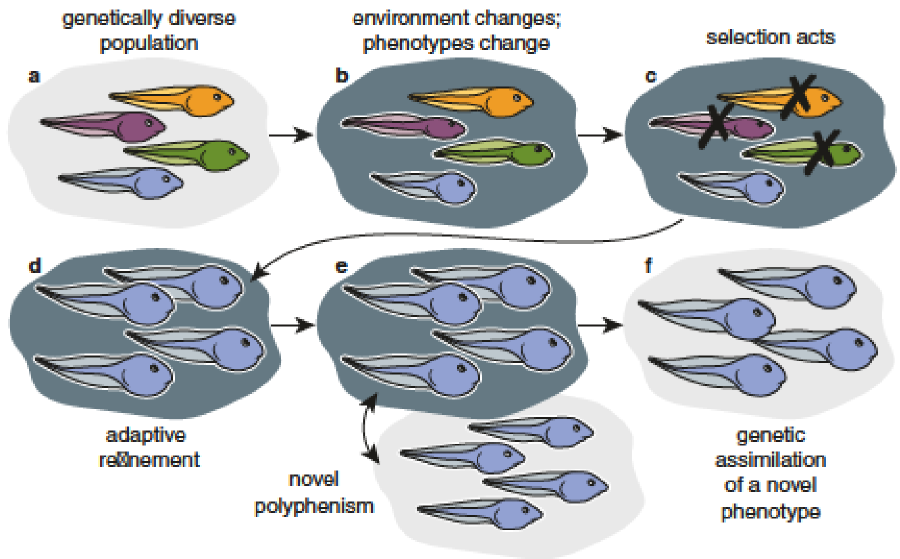
For the past few decades, I have been evaluating plasticity-led evolution in a fascinating group of amphibians: spadefoot toads (hereafter, simply spadefoots). Spadefoots are found throughout the United States and northern Mexico, even in deserts. To cope with arid environments, spadefoots have evolved numerous adaptations. Among these is that the tadpoles of several species have evolved a unique form of plasticity: Although they normally develop into a round-bodied omnivore morph, if they eat meat (for instance, fairy shrimp), they may develop into a carnivore morph. This form, which specializes on meat, sports a large head, a serrated keratinized beak, and a short gut. Because they develop rapidly, carnivores are more likely to escape a drying pond.

To test whether this novel carnivore morph evolved through plasticity-led evolution, my graduate students—Cris Ledón-Rettig, Nick Levis, and Andrew Isdaner—and I have studied different species and populations of spadefoots that appear to represent different stages in the evolution of the carnivore morph. Using this sort of comparative approach to infer the possible stages in the evolution of a feature of interest has a long and rich tradition in evolutionary biology and was used extensively by Darwin. For our studies, we focused on five different species and populations of spadefoots: *Scaphiopus couchii* and *Scaphiopus holbrookii*, which do not produce the carnivore morph; *Spea bombifrons* and

Spea multiplicata, which both produce thecarnivoremorphaspartofapolyphenism; and certain populations of *Spea bombifrons*, which appear to be fixedforproducingthecarnivoreonly; thatis,thecarnivoremorphappearsto have under gone genetic assimilation inthesepopulations.

Whenwecomparedtadpolesreared on the plant-based diet of omnivores or the meat diet of carnivores, we found subtle but significant diet-induced plasticity in both *Scaphiopus* species. Becausethesetwospeciesexhibit the ancestral condition, in that they do not produce carnivores, this findingsuggeststhatpreexistingplasticity might have been present in the ancestors of the modern-day genus *Spea*, the group that does produce carnivores. We also found evidence of adaptive refinement of this plasticity in both *Spea* species; for example, they grew equally well on plants and meat, in contrast to both *Scaphiopus* species, which tended to grow poorly on a meat-based diet. Finally, we found further refinement of the carnivoremorphin*Speabombifrons*populationsthatproduceonlycarnivores.For example, these populations produced a version of the carnivore morph that wascompetitivelysuperiortothecarnivoresproducedbyanyotherspecies or populations of *Spea bombifrons*. We are attempting to identify the genes involved in producing this unique morph to understand what genetic pathways may have mediated the changesweobservedinspadefoots.

Thus, our research provides support for plasticity-led evolution from natural populations. But ours is by no means the only study to support this idea. Indeed, plasticity-led evolution has been documented in speciesasdiverseasbacteriaandsnakes. Moreover,plasticity-ledevolutionhas beenimplicatedinmajorevolutionary events,suchastheevolutionofmulticellularity.Inshort,plasticitymightbe crucialinfosteringevolutionarydiversificationandinnovation.



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Inthisexampleofplasticity-ledevolution,ageneticallyvariablepopulationoftadpoles(*a,differentcolorsrepresentdifferentgenotypes*)experiencesanenvironmentthatinducesnovelphenotypes (*b,representedbywhiteoutline*),anddifferentgenotypesalsoproducedifferentphenotypes(*representedbydifferentbodyshapes*).Selectioncanactonthisformerlycrypticgeneticvariationanddisfavorgenotypesthatproducepoorlyadaptedphenotypes(*c*).Adaptiverefinementofthefavored phenotype(*d*)canultimatelyresultineitheranovelpolyphenism(*e*)orgeneticassimilation(*f*).

TransgenerationalPlasticity

Perhaps the most controversial topic inplasticityresearch—becauseitraisesthevexingissueofhowweshould define evolution—is whether specific plasticresponsescanbepassedtooffspring. In other words, can a parent pass to its offspring any features that theparentacquiredduringitslifetime through plasticity? Such *transgenerational plasticity* is sometimes dubbed the *inheritanceofacquiredcharacters* and attributed to the early 19th-century FrenchscholarJean-BaptisteLamarck. However, the notion that acquired features could be passed to offspring antedatesLamarckandwaswidelyaccepted by many natural historians in histime.Forexample,in *OntheOrigin ofSpecies*, Darwin wrote, “I think that there can be no doubt that increased use of certain parts of our domestic animals has strengthened and enlarged them, and disuse diminished them, and that such modifications havebeeninherited.”

Thepersoncreditedwithdisproving theinheritanceofenvironmentallyinducedtraitswastheGermanbiologist AugustWeismann.Inthe1880s,Weismann cut the tails of mice in half for fivegenerationsandobservedwhether their offspring acquired a shortened tail;unsurprisingly,notasinglemouse was born with a rudimentary tail. From this experiment, as well as detailed observations of how embryos developed, Weismann concluded that “the improvement of an organ in the courseofgenerationsisnottheresult ofasummationoftheresultofpractice ofindividuallives,butofthesummationoffavorablegeneticfactors.” After Weismann,theinheritanceofacquired charactersneveragaingainedfulltractioninbiology.

> **Evolutionarybiologistshavelong grappledwithunderstandinghow plasticityimpactsevolution.**

However, it is becoming increasingly clear that biological information can be conveyed through various nongenetic factors that are not specified by DNA sequence, including factors induced by the environment through plasticity. Indeed, parents often differentially endow their seeds, eggs, or offspring with materials or information that these parents acquired from the environment. Among the best-studied examples is *DNA methylation*, where the addition

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Plasticity-led evolution has been implicated in the origins of numerous novel features such as (*clockwise from upper left*) nitrogen-fixing cells in cyanobacteria, invasiveness in sunflowers, the rattle in rattlesnakes, and distinct castes in ants.

of a methyl group (CH_3) to components of the DNA can influence the activity of the genes on that strand. Although some methyl tags are themselves encoded by DNA, environmental factors, such as diet or stress, often induce them. Once induced, the individual's offspring can even inherit these epigenetic factors and associated altered traits (note that the term *epigenetic* refers to the effects of certain types of molecules, such as methyl groups and RNA, that interact with DNA to influence gene expression. Thus, epigenetic describes a molecular mechanism of plasticity). During replication of DNA before cell division, specialized enzymes can copy a methyl tag from the parent strand onto the daughter strand. In this way, an offspring can inherit a feature that its parent acquired during its lifetime through plasticity. In some cases, epigenetic information can even be incorporated into the germline of a group of organisms. For instance, a recent fascinating study by Elizabeth O'Brien of the QIMR Berghofer Medical Research Institute in Australia has shown that environmentally induced changes to RNA can be transported from the mouse brain, where it was initially induced, to the germline and, ultimately, to offspring.

In sum, genes are not the only factors transmitted across generations and should not be viewed as the sole cause of heredity. Although it is unclear how common and how durable transgenerational plasticity is in natural populations, it is clear from the examples outlined above that environmentally induced traits can sometimes be inherited. Understanding when and how transgenerational plasticity occurs is a crucial research frontier of biology with vast implications for evolution and human health.

Plasticity and Evolutionary Theory

Those who study evolution have long struggled with incorporating plasticity into their intellectual framework. This debate over plasticity's role in evolution has led some, such as the evolutionary biologists Kevin Laland of the University of St. Andrews in Scotland and Armin Moczek of Indiana University Bloomington, to suggest that integrating plasticity into evolutionary biology will require a major extension of the modern synthesis. Does evolution need a makeover?

The answer is not a simple "yes" or "no." Many aspects of plasticity fit comfortably within existing evolutionary theory. For example, both the buying time and plasticity-led evolution hypotheses entail selection acting on heritable phenotypic variation that affects fitness, which is the standard model of adaptive evolution that has held since Darwin. Indeed, West-Eberhard has argued that plasticity must be recognized, along with genes, as being central to adaptive evolution for this simple reason: Adaptive evolution requires heritable changes due to selection; selection requires phenotypic variation; and all phenotypic variation is generated by inputs from genes and the environment. Therefore, plasticity—developmental responsiveness to environmental inputs—has long been part of standard evolutionary theory, even if it is not explicitly acknowledged as such.

Other aspects of plasticity do not fit as well within existing evolutionary theory. Foremost among these is the transgenerational plasticity described in the previous section. On the surface, transgenerational plasticity does not appear to violate any fundamental tenets of evolutionary biology. After all, Darwin's theory says nothing about the mechanism of inheritance, because Darwin knew nothing of genes. Nevertheless, Darwin was still able to develop a robust theory that has withstood the test of time because, as the late evolutionary biologist John Maynard Smith emphasized, adaptive evolution merely requires that "like begets like," regardless of how this process of inheritance occurs. Yet, if the environment of its ancestors also shapes an individual's phenotype—as would happen with transgenerational plasticity—then we cannot assume, as many often do, that the individual's developmental response to its environment is scripted by its genotype.

Essentially, knowledge of plasticity can enhance our understanding of evolution by emphasizing how the environment can select phenotypic variation and help generate that variation in the first place. Consequently,

Plasticity might be crucial in fostering evolutionary diversification and innovation.

incorporating plasticity into evolutionary thinking may help illuminate a broader array of evolutionary phenomena. Consider the following three phenomena.

First, as our research on spadefoots has shown, plasticity may help explain the origins of novel, complex features. Although novelty can undoubtedly arise via changes in the genome such as mutation, features initially expressed through plasticity may be especially likely to undergo adaptive refinement. This is because features induced by the environment are typically expressed by many individuals simultaneously, and they are often associated with an environment in which they are adaptive. Increasing evidence suggests that numerous complex traits, ranging from specialized cells in bacteria to distinct castes in social insects, may have started as plastic responses, indicating that these novel features have arisen through plasticity-led evolution.

Second, plasticity may help explain rapid evolutionary change. Although evolutionary change wrought by mutations can occur rapidly, the circumstances for this are limited: Beneficial mutations are scarce, they initially affect only a single individual and its immediate descendants, and therefore they are often slow to spread through a population. By contrast, features induced by the environment have characteristics that potentially hasten evolution. As we have seen, they are typically expressed in many individuals at once, and they are often associated with an environment in which they are beneficial. Essentially, plasticity may jump-start evolution. Plasticity's ability to hasten evolution may become increasingly important when natural environments are changing ever more rapidly because of changes wrought by humans.

Finally, plasticity can help explain a pervasive pattern among fossil and living organisms: *convergent evolution*, where similar features evolve independently in different evolutionary lineages (such as dolphins and sharks). Such convergence is generally assumed to arise when similar selection pressures acting on randomly generated mutations produce similar features. However, unrelated organisms experiencing similar environments often produce similar features through plasticity. For example, in response to low light levels, many plant species facultatively produce broader leaves, and in response to eating meat, many animals facultatively produce a shorter gut. If these induced traits undergo genetic assimilation, the result would be convergent evolution. Consistent with this hypothesis, among several groups exhibiting convergent evolution, the traits subject to convergent evolution are plastic in close relatives. Thus, evolution may often, but not always, proceed through genetic changes that stabilize what were initially plastic responses to produce a pattern of convergent evolution.

A broader understanding of phenotypic plasticity will affect all of biology, as it will require that researchers confront two complexities of biological systems that biologists often ignore: that most traits emerge from the interplay of an individual's genes with its environment, and that phenotypic flexibility is the rule rather than the exception. Greater appreciation of this important but frequently misunderstood phenomenon promises to provide far-reaching new insights into not only evolutionary biology but also fields as diverse as the biomedical sciences and conservation biology.

Practical Applications of Phenotypic Plasticity

Predicting evolutionary responses to climate change. Plasticity may help determine which species will "win" and which will "lose" under anthropogenic environmental change.

Optimizing agricultural yields. In developing crops, one must know how to reduce plasticity to ensure that the same crop produces high yields in different regions experiencing different environments.

Understanding the causes of nonheritable birth defects (teratogens) in both humans and nonhuman animals. Changes in the environment can disrupt development. It is estimated that 2 percent to 5 percent of human infants are born with an anatomical abnormality, as are an increasing number of other animals. Many such abnormalities are triggered by environmental factors.

Clarifying the evolutionary causes of nutrition-related disease in humans. Nutrition-induced plasticity is common in humans, and it can lead to obesity and obesity-related diseases. The most dangerous form is exaggerated development of visceral adipose tissue (VAT). Some have suggested that selection favored increased investment in VAT in individuals who were food deprived when young as adaptive anticipatory plasticity to mitigate malnourishment in adulthood.

Understanding the human brain. In response to changes in the environment, brains can rewire synaptic interactions. Such neuroplasticity can even allow neurons to compensate for injury and disease.

Wikipedia; publicdomainvectors.org; freesvg.org; Mark Sykes/Flickr.com

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