III.13

Biochemical and Physiological Adaptations

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Organisms can thrive in diverse environments by evolving biochemical processes to tolerate extreme conditions or to avoid these extremes by regulating internal conditions. Both tolerance and regulation impose costs, often expressed as trade-offs with other traits that affect fitness. By analyzing these trade-offs, one can predict how natural selection will shape physiological strategies in particular environments. Our understanding of physiological adaptation has been tested through comparative analyses of populations along environmental clines and experimental evolution of populations in the laboratory. These approaches have often led to surprising insights, suggesting that we can better understand physiological adaptation by also considering processes such as mutation, drift, and migration. Although biologists still have much to learn about physiological adaptation, our current knowledge has already helped to predict biological impacts of global change.

GLOSSARY

Abiotic Factor. A variable that describes a physical (nonliving) characteristic of the environment, such as temperature, humidity, or pH.

Extreme Environment. An environment in which some abiotic factor approaches a value that limits an organism's survival or reproduction.

Generalist. An organism that tolerates a wide range of environmental conditions.

Heritability. The proportion of phenotypic variation that results from genetic variation among individuals.

Optimality Model. A mathematical model that defines the relationship between a phenotype and fitness in a specified environment. This relationship can be used to find the phenotype that maximizes fitness (the optimal phenotype).

Osmolyte. A soluble compound affecting the osmosis of a cell.

Regulation. The act of maintaining an internal state that differs from the state expected if the organism were to exchange energy or materials passively with its environment.

Specialist. An organism that tolerates only a narrow range of environmental conditions.

Tolerance. The ability to survive and reproduce in a given environment.

Trade-off. A decrease in the quality of one trait stemming from an increase in the quality of another trait.

1. PHYSIOLOGICAL DIVERSITY

Earth provides a home for millions of species, some residing on its surface while others dwell within dark crevices, loose soils, or deep oceans. Each of these species represents a unique way of accomplishing a single goal: persistence. In the process of achieving this goal, organisms must do more than just survive and reproduce; they must also forage, grow, and develop until they have acquired sufficient size, experience, and resources to leave offspring. These functions rely on a suite of biochemical processes that are common to all organisms, as well as specialized processes that have evolved within certain types of organisms (e.g., aerobic respiration, photosynthetic nutrition, neuromuscular communication). The biochemistry of life depends on abiotic factors such as temperature, pressure, and pH. Yet life occurs in just about every environment on our planet, spanning an amazingly broad range of conditions.

Although life occurs everywhere, no species does so. Each species functions under a limited range of conditions, referred to as its *physiological tolerance*. The relationship between a species' tolerance and its distribution is most evident from a global perspective. Tropical waters are known for their great diversity of fish, most of which swim very well at temperatures around 25 °C. Cool a tropical fish by just a few degrees, and its ability to swim also declines; for instance, the zebra fish (*Danio rerio*) cannot swim well at temperature below 15 °C. Yet close to the poles, many species of fish patrol icy waters that rarely exceed 0 °C. Despite their incredibly cold bodies, these fish show no sign of stress. Yet if one were to warm these fish just a few degrees, they would become stressed! Thus, environmental stress is relative; conditions that stress some species enable other species to thrive. Clearly, the different thermal tolerances of tropical and polar fish reflect adaptation to their local environments. Similar patterns of adaptation exist along gradients of humidity, salinity, acidity, toxicity, and pressure.

Species adapt to environmental stress in two ways. As in the case of polar fish, a species can acquire mutations that enable it to tolerate extreme internal conditions (e.g., low temperature). The evolution of physiological tolerance involves changes in the structures or concentrations of proteins, which in turn alter membranes, tissues, and organs. Alternatively, a species can acquire mutations that enable it to regulate its internal conditions within tolerable limits (e.g., thermoregulation). Some of the most effective forms of regulation involve not only physiology but behavior and morphology as well. Depending on the circumstances, natural selection can enhance tolerance, regulation, or both. Although polar fish evolved the ability to tolerate subzero body temperatures, polar mammals evolved the ability to maintain body temperatures that greatly exceed the temperatures of their surroundings. In reality, tolerance and regulation evolve together according to their relative costs and benefits to a species.

This chapter outlines four themes emerging from studies of physiological adaptation. First, optimality models help biologists understand how trade-offs shape physiological diversity (see chapter VII.3). Second, biochemical mechanisms of tolerance and regulation determine the trade-offs during physiological adaptation. Third, physiological variation within and among species often reflects adaptation to local environmental conditions. Finally, observed physiological strategies sometimes differ from optimal physiological strategies because of genetic constraints (see chapter III.8). Although these themes are illustrated through examples, the brevity of this article precludes a detailed treatment of many fascinating cases of physiological adaptation. Interested readers should consult the references that follow this article for additional perspectives on evolutionary physiology.

2. HOW DO WE KNOW THAT PHYSIOLOGICAL VARIATION IS ADAPTIVE?

How do we know that physiological diversity resulted from natural selection rather than some nonadaptive process? To be confident, we must compare the observed patterns with those predicted by theoretical models. Optimality models have been invaluable in this endeavor. Such models tell us the selective pressures on physiological traits given a set of hypothetical constraints, usually referred to as trade-offs. A satisfactory match between a model's predictions and a researcher's observations supports the idea that the physiological variation is adaptive. A substantial mismatch indicates that either the variation is nonadaptive or that our evolutionary model omits some important constraint.

Physiologists have used two approaches to test the predictions of optimality models. The oldest and most widely adopted approach is to compare the traits of species that evolved in different environments (see chapter II.7). In recent decades, comparative analyses have been aided by statistical methods that control for the effects of common descent; since any two species have inherited some phenotypes from a common ancestor, common descent can inflate or mask signals of adaptation. The second approach is to expose experimental populations to controlled environments and then quantify the genetic divergence of traits (see chapter III.6). Both comparative analysis and experimental evolution have advantages and disadvantages. Comparative analysis tells us how physiology has evolved in complex environments, but it cannot disentangle the myriad of factors that covary among environments. Experimental evolution isolates hypothetical selective pressures by manipulating some environmental factors while controlling others; nevertheless, this approach is practical only for studying species with short generations that are easily raised in laboratories. Thus, comparative analysis and experimental evolution are complementary approaches to testing hypotheses about physiological adaptation.

3. BIOCHEMICAL MECHANISMS INFORM MODELS OF PHYSIOLOGICAL ADAPTATION

To model the trade-offs constraining physiological adaptation, we must know the mechanisms by which extreme environments affect biochemical processes. Abiotic conditions can alter the structures of proteins in ways that inhibit chemical reactions. Since a protein's structure depends on weak bonds between amino acids, changes in conditions within cells can disrupt this structure. Yet, modifying the sequence of amino acids that form a protein can improve the protein's function under extreme conditions. As an example, consider the modifications that improve function at extreme temperatures. Amino acids that increase the stability of a protein improve function at high temperatures, whereas those that decrease stability improve function at low temperatures. Thus, biochemical adaptation to one thermal extreme necessarily results in maladaptation to the other. Adaptation to osmotic pressure imposes a similar trade-off. To limit water loss in a hyperosmotic environment, organisms must maintain high concentrations of solutes that are compatible with proteins. In a hypo-osmotic environment, however, high concentrations of solutes would cause cells to swell with water, reducing the concentrations of chemical reactants and potentially causing death.

Can species evolve to tolerate wide ranges of conditions? One way to become a generalist is to produce multiple forms of the same protein, each capable of functioning under different conditions; however, an organism would have to invest the energy required to synthesize additional proteins, which would reduce the energy available for other activities. Another strategy would be to make one type of protein at a time and modify the concentrations of each protein as conditions change. In this case, energy would still be needed to turn over proteins on a regular basis. Given a limited amount of energy, biochemical adaptation to a wide range of conditions would compromise performance under any single condition. In other words, a jack of all environments would be a master of none.

Enhanced regulation imposes an energetic cost that also mediates trade-offs in performance. Regulation of internal conditions involves metabolic processes that rely on the energy stored in chemical bonds, such as the covalent bonds of macromolecules. Mammals and birds regulate their body temperature by catabolizing carbohydrates to generate heat. Many marine fish regulate their osmotic pressure by coupling the catabolism of adenosine triphosphate to the transport of salts across the epithelia of the gills. Terrestrial organisms reduce their rates of water loss by forming a water-resistant cuticle. Each of these forms of regulation involves cellular machinery that requires energy to produce and maintain; therefore, an organism possessing this machinery would gain a physiological advantage in a stressful environment but suffer an energetic disadvantage in a benign environment.

4. ADAPTIVE VARIATION IN TOLERANCE

Consistent with the biochemical mechanisms described above, current optimality models assume that the ability to tolerate one environmental extreme leads to an inability to tolerate another. This hypothetical constraint prevents the evolution of a species that performs extremely well under all conditions. Given this trade-off, two predictions emerge. First, species should evolve to perform best under the conditions that they experience most frequently. Second, species should evolve to perform over the narrowest range of conditions needed to persist in their environment. Thus, constant environments would favor specialists, whereas variable environments would favor generalists (see chapter III.14).

These predictions about physiological adaptation have been tested extensively by comparing species distributed along latitudinal gradients. Since the mean temperature decreases and thermal variation increases from the equator to the poles, we should expect thermal tolerance to vary among species at different latitudes. Consistent with this expectation, tropical species tolerate high temperatures better, but low temperatures worse, than do temperate or polar species. Moreover, in many groups of plants and animals, species from higher latitudes tolerate a wider range of temperatures. Broad geographic patterns of tolerance have also been observed for other abiotic factors, such as moisture, salinity, and pH.

These patterns of environmental tolerance suggest that a species transplanted to a novel environment could not function as well as one that evolved in that environment. In fact, many experiments have been conducted in which (1) organisms were reciprocally transplanted between distinct environments and (2) the performances of native and transplanted individuals were compared. In one of these experiments, Amy Angert and her colleagues moved two species of plants (*Mimulus cardinalis* and *Mimulus lewisii*) that normally occur at different altitudes. Native individuals outperformed transplanted individuals, indicating that adaptation to high altitude resulted in maladaptation to low altitude (and vice versa). Subsequent experiments by Angert and others confirmed that temperature was an important factor. In the laboratory, individuals from high altitude grew better at low temperature than did individuals from low altitude. In a field experiment, genotypes grown at low altitude survived according to their ability to photosynthesize at high temperatures; however, greater photosynthesis came at the expense of cold tolerance, leading to selection against these genotypes at high altitude. Although the biochemical basis of adaptation differs from case to case, the majority of transplant experiments have revealed adaptation of tolerance along abiotic gradients.

Despite the wealth of evidence from comparative analyses, recent insights from experimental evolution have challenged our notions about the adaptation of tolerance. Model organisms—representing species from all kingdoms of life—have been exposed to a multitude of environmental conditions in the laboratory. And in all cases, some degree of physiological adaptation occurred. One of the most widely studied species, *Escherichia coli*, adapts readily to thermal, acidic, and nutritional stresses. Some experimentally evolved populations have been screened for mutations that conferred tolerance. Shaobin Zhong and his colleagues found that adaptation to nutritional stress requires mutations to downregulate proteins that transport the usual source of carbon and upregulate proteins that transport an alternative source. Adaptation to an environment containing only lactulose consistently involved duplication of genes encoding a protein that transports this substrate. By contrast, adaptation to methyl-galactoside involved deletion of a particular region of the genome that, if present, suppresses the expression of a protein that transports methyl-galactoside. Exposure to a mixture of these substrates nearly always caused the evolution of a mixture of specialists, each of which used one of the substrates. This result accords with the common assumption that generalization imposes an energetic cost that should be avoided when possible. Unfortunately, many other cases of experimental evolution conflict with this theoretical view. In most experiments that exposed populations to fluctuating conditions, adaptation led to a population of generalists that could outperform specialists. Once biologists understand the biochemical mechanisms that enable certain genotypes to succeed over a wide range of conditions, they will need to revise current models of optimal tolerance accordingly.

5. ADAPTIVE VARIATION IN REGULATION

When tolerance cannot evolve because of costs or constraints, a species can regulate its internal state to persist in extreme environments. The benefit of physiological regulation depends on an organism's tolerance of environmental conditions. A specialist, which performs well only within a narrow range of conditions, would benefit greatly from regulation. The cost of regulation depends on the time and energy required to maintain an internal state that deviates from the external one. From an optimality perspective, we should expect either a high benefit or a low cost to cause the evolution of effective regulation.

Much evidence of adaptive regulation comes from studies of thermal and hydric states, which often depend on one another. In particular, mammals and birds provide outstanding examples of adaptive regulation in the face of varying costs. In cold environments, these animals rely on metabolic reactions to generate the thermal energy needed to maintain warm bodies (*endothermy*). In hot environments, excess thermal energy can be dissipated through the evaporation of water. For many species, these regulatory processes result in a nearly constant body temperature. Nevertheless, both mammals and birds adjust the intensity of thermoregulation when either energy or water becomes scarce. Experimental manipulations of feeding rate, ambient temperature, and thermal insulation have shown that mammals and birds let their bodies cool considerably when maintaining an elevated temperature becomes energetically costly. Furthermore, these animals let their bodies warm to unusually high temperatures when dehydrated. This tradeoff between balancing thermal and hydric states also occurs in organisms that rely primarily on solar radiation to thermoregulate (*ectothermy*).

As with physiological tolerance, physiological regulation varies adaptively along abiotic gradients. Comparisons of populations within and among species of *Drosophila* have generated a comprehensive view on the regulation of water loss, reinforced by studies of experimental evolution. In general, flies from temperate environments resist desiccation better than do flies from tropical environments. This resistance to desiccation comes from enhanced regulation of water loss rather than enhanced tolerance of dehydration. Allen Gibbs and his colleagues used experimental evolution to discover mechanisms underlying the adaptation of water regulation in *Drosophila melanogaster*. Populations exposed periodically to dry conditions evolved genotypes that develop relatively long chains of hydrocarbons in their cuticles, a biochemical strategy thought to reduce water loss. This example illustrates the complementary nature of comparative and experimental approaches to the study of physiological adaptation.

6. ADAPTIVE ACCLIMATION

Organisms benefit greatly from the ability to adjust their physiology in response to environmental conditions, a process usually referred to as *acclimation*. In a fluctuating environment, acclimation enables an organism to specialize for conditions that will likely occur in the future given conditions of the past. But acclimation involves costs as well as benefits. Energy must be expended to restructure cells and tissues as environmental conditions change. Moreover, tuning one's physiology to match expected conditions involves an element of risk beyond the commitment of energy; if past conditions relate poorly to future conditions, the organism might commit to the wrong strategy! In an unpredictable environment, natural selection would favor generalists that do not acclimate during environmental change.

Since species differ in their ability to acclimate, we can ask whether these differences reflect adaptation to the variability and predictability of their environments. Comparative studies of acclimation are less common than other studies of physiology, but enough data exist to challenge our current notions about optimal acclimation. Since environmental variation increases with increasing latitude, species at high latitudes should evolve a greater capacity for acclimation. Consistent with this expectation, rodents from high latitudes can adjust the length of their intestine more readily than can rodents from low latitudes. The most flexible species of rodents also occupy the widest range of habitats. Still, other comparisons failed to support the view that abilities to acclimate have adapted to local environments. For example, both tropical and temperate genotypes of *Drosophila melanogaster* readily adjust their tolerances of high and low temperatures in the lab, although these genotypes experience very different levels of thermal variation in nature. Likewise, other species of flies adjust their rates of water loss when raised under dry or humid conditions, regardless of whether they come from environments that experience such conditions. The widespread capacity for acclimation in these species could reflect dispersal among distinct environments; dispersal leads to variation in environmental conditions among generations, which strongly selects for genotypes that can tune their physiology to current conditions.

Experimental evolution enables researchers to control or manipulate environmental variation, to see whether adaptation involves a change in the ability to acclimate. In a recent experiment, Brandon Cooper and his colleagues compared populations of *Drosophila melanogaster* exposed to either constant or fluctuating temperatures for more than 30 generations. These populations diverged such that genotypes from the fluctuating environments were better able to adjust their cellular membranes to developmental temperature. The specific adjustment, involving the ratio of two phospholipids, was the very kind expected to confer greater performance in either hot or cold environments. This finding supports the view that environmental variation promotes the evolution of acclimation.

7. CONSTRAINTS ON PHYSIOLOGICAL ADAPTATION

When we use an optimality model to predict physiological variation, we assume that nonadaptive processes have not constrained adaptative ones. Processes such as mutation, genetic drift, and gene flow can slow adaptation in two ways. First, some of these processes can reduce the amount of genetic variation in a population. Second, all of these processes can increase the frequency of maladaptive alleles in a population. Both factors have influenced the evolution of physiology.

How does genetic variation constrain physiological adaptation? Adaptation depends not only on selection but also on heritability. If the physiological variation among individuals was caused by environmental factors rather than genetic factors, selection cannot produce evolutionary change. In general, physiological variation is no less heritable than morphological variation; nevertheless, the type of physiological variation present within populations does not always reflect the type that enables the evolution of optimal phenotypes. For example, consider a species that occurs throughout a wide range of latitudes. Current optimality models predict that adaptation would lead to tropical genotypes that perform best at high temperatures and temperate genotypes that perform best at low temperatures. But how likely is this form of adaptation when one considers genetic constraints? Specializing for function at extreme temperatures might require mutations of hundreds of genes, which would take a very long time to accumulate. Instead, adaptation sometimes takes a more convenient course, as illustrated by the studies of Atlantic silversides (*Menidia menidia*) conducted by David Conover and his colleagues. Northern and southern populations of these fish experience different temperatures in nature, but both populations grow best at the same temperature in the lab. Even more surprising, northern genotypes outgrow southern genotypes over a wide range of temperatures, including those temperatures more common in the south. Why do these apparently superior genotypes not spread throughout the entire range? The answer lies in understanding the cost of their rapid growth. These fish grow rapidly by consuming large amounts of food, which reduces swimming speed and increases predation risk. The benefit of rapid growth outweighs this cost in highly seasonal environments, but the reverse seems true in less seasonal environments; therefore, trade-offs in fitness between environments exist even when trade-offs in growth do not. The adaptation of feeding behavior in silversides likely reflects insufficient genetic variation to adapt biochemical functions to low temperature.

Gene flow between distinct environments also slows the adaptation of physiology by increasing the frequency of maladaptive alleles (see chapter IV.3). This phenomenon can operate even on very small spatial scales. For example, many species of plants and fungi that live in contaminated soils have evolved biochemical mechanisms to regulate the absorption of toxic metals. These species generally exhibit clines in metal tolerance between contaminated and uncontaminated sites. Experiments have shown that alleles conferring greater fitness at contaminated sites reduce fitness at uncontaminated sites. Yet the close proximities of these sites sometimes enable deleterious alleles to persist through gene flow. Gradual clines in metal tolerance have been observed along transects running parallel to seed dispersal, whereas sharp clines have been observed along transects running perpendicular to seed dispersal. Although dispersal can help to establish populations in stressful environments, ultimately this process limits physiological adaptation to these environments.

8. IMPLICATIONS FOR GLOBAL CHANGE BIOLOGY

The adaptation of physiology—in the past, present, and future—has significant consequences for the persistence of species in a changing environment. Given the physiology diversity highlighted in the preceding sections, biologists have become keenly aware of the need to consider how physiological adaptation influences the dynamics of populations and the ranges of species. Most models that incorporate physiological diversity have focused on the responses of species to global climate change. Changes in temperature, humidity, and precipitation have altered and will continue to alter the geographic distributions of species. Importantly, physiological adaptation can ameliorate or exacerbate these effects. For example, a model developed by Michael Kearney and his colleagues indicates that the Australian distribution of the dengue mosquito (*Aedes aegypti*) is limited by moisture in the north and temperature in the south. Their model also shows that adaptation of desiccation resistance during the next few decades could enable this species to spread throughout northern Australia. Predictions of this kind depend not only on the selective pressures created by climate change but also on the constraints that limit physiological adaptation (see section VII). Models that consider physiological adaptation should become increasingly relevant to global change biology.

FURTHER READING

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