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Phenotypic Plasticity

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Phenotypic plasticity is the ability of an individual to express different features under different environmental conditions. Examples of plasticity surround us: plants have broader leaves when grown in shady conditions, and animals are smaller when they develop in crowded conditions. Although some of these changes reflect unavoidable consequences of adverse conditions, many of them are the product of natural selection molding an organism's ability to survive and reproduce in a world whose conditions vary from time to time and from place to place. Put another way, many examples of phenotypic plasticity reflect the evolution of a developmental system that attempts to produce different traits under different conditions because no single trait is best suited for all conditions. Plasticity facilitates a species' ability to occupy a variety of habitats, persist in uncertain environments, and stabilize its interactions with other species whose incidence and numbers change over time and across space.

GLOSSARY

- carapace.** The hard outer shell surrounding the bodies of small animals such as waterfleas and larger animals such as turtles.
- diapause.** A state of arrested development in which the animal can survive long periods of challenging conditions such as low temperatures or drought by lying dormant.
- ectothermic animals.** Animals that use external sources of heat for metabolism and whose rates of metabolism are closely linked to external temperatures, such as invertebrates, fish, amphibians, and reptiles.

fitness. The number of offspring an individual leaves behind for the next generation; fitness has two major components, survival (or length of life) and reproductive rate.

numerical stability. A steady-state equilibrium in population size, that is, numbers of individuals, to which a system will return if it is perturbed; stability in predator-prey systems refers to the numerical stability of both predator and prey that allows them to coexist indefinitely.

phenotypic plasticity. The ability of an individual to express different features under different environmental conditions.

1. INTRODUCTION

Phenotypic plasticity is the ability of an individual to express different features under different environmental conditions. This "adaptive plasticity" is one of the most remarkable products of Darwinian evolution. For adaptive plasticity to emerge, the developmental machinery to build different traits must be integrated with a sensory system that detects reliable cues about the prevailing environmental condition so that suitable traits are expressed in a timely manner. Adaptive plasticity is an interesting topic for evolutionary biology, but it is also an important topic in ecology. One reason is that plasticity can enable a species to cope with highly seasonal environments or occupy diverse habitats. But more subtly, plasticity can have a substantial effect on a variety of ecological processes and thereby act as an important influence on which species we see where and at what population sizes.

2. THE SPECTRUM OF PHENOTYPIC PLASTICITY

Phenotypic plasticity can be either reversible or irreversible. The most obvious examples of reversible changes are behavioral responses to environmental conditions. For example, tadpoles change their foraging patterns in response to the presence of predators. When predators

are removed, the tadpoles adjust accordingly. Other well-known reversible responses include physiological changes such as the increase in mitochondrial density in terrestrial vertebrates in response to experiencing lower oxygen levels and the changes in specific fatty acids incorporated into animal cell membranes in response to changing thermal conditions. Morphological changes can also be reversible: the gills of aquatic salamanders increase or decrease in response to oxygen levels in the water, and vertebrate muscles change in form and density in response to the amount of use they receive.

As one might expect, reversible plasticity appears when environmental conditions change, often within an individual's lifetime. In most cases, individuals retain the ability to change their features for most of their lives. The exception to this rule is diapause in insects and other arthropods. Diapause is a state of arrested development in which the animal can survive long periods of challenging conditions such as low temperatures or drought by lying dormant. When conditions improve, the animal breaks diapause and resumes normal activity and development. A species can enter diapause in only one stage, for example, eggs in crickets and larvae in beetles, and once broken, diapause cannot be reentered.

Irreversible changes occur trivially when an organism adjusts the timing of a life history transition in response to environmental circumstances. Once an annual plant initiates flowering in response to its lighting conditions, there is no going back. Less trivially, irreversible changes are reflected in features that, once expressed, are not altered regardless of how conditions may change. For example, waterfleas in ponds develop spines and a thicker carapace in response to the presence of a predatory fly larva in the water; once developed, the carapace is not altered appreciably even if the predators disappear. A species of African acacia develops long spines on its stems in response to being browsed by giraffes and elephants; these spines remain for the lifetime of the tree, even if it never suffers from additional browsing.

Irreversible plasticity appears when environmental conditions are less volatile and less likely to change drastically within the lifetime of an individual. In many of these cases, there is a narrow window of development within which the individual is sensitive to the cues in the environment that trigger the expression of the feature. Outside of that window, the cues elicit no response. When these narrow windows of sensitivity exist, the individual is committing itself for the future in response to conditions in one relatively short period.

Whether reversible or irreversible, plasticity is expressed in response to a wide range of environmental

factors. Some factors act ubiquitously; nearly all plants alter the expression of shoots, leaves, and flowers in response to variation in their lighting environments, and most animals alter development in response to variation in their thermal environments. Classes of biotic agents—predators, pathogens, potential competitors—also induce plastic responses. In some cases, the cue for the response is direct: the African acacia develops spines after it has been browsed. In others, the cue is indirect: waterfleas develop thicker carapaces in response to a chemical cue that alerts them to the presence of a larval midge predator, even before there is any attack on an individual waterflea.

The many examples of plasticity in nature might suggest that just about any feature of an organism can be phenotypically plastic and just about any environmental condition can induce a plastic response. This is true if one looks at all of nature's examples en masse; every trait responds to some environmental factor, and just about any environmental factor imaginable affects some trait in some species. But in a very important sense, it is not: plasticity can be quite specific. To be sure, there are general patterns of plasticity; nearly all ectothermic animals make larger eggs at lower temperatures. But the more striking observation is that the development of certain traits responds in specific species to specific cues; traits in a species that respond to one environmental agent may not respond to a different one, and the same features in different species may not respond to the same agent. Put another way, when one says "Trait X is plastic," one needs to specify in which species and in response to variation in which environmental condition.

There are several striking examples of this specificity. Damselfly species that coexist with fish behave differently in the presence of fish than in their absence, but species that do not coexist with fish fail to respond to their presence and are more likely to be eaten. Plasticity can even be specific at the population level; wild parsnip populations with a history of heavy herbivory respond to leaf damage by releasing compounds toxic to insect herbivores, whereas populations without a history of heavy herbivory do not.

Even more subtly, plasticity can be quite precise. That is, a trait may respond only to a particular range of variation in an environmental factor, and the same trait in different species may respond to a different range of variation in that same factor. Insect diapause is a classic example: populations of the same species at different latitudes enter diapause in response to different combinations of temperature and day length.

The specificity and precision of so much phenotypic plasticity suggest that it is not merely an ineluctable

consequence of animal or plant physiology but a well-honed evolutionary response to variable environments of a particular kind.

3. THE EVOLUTION OF ADAPTIVE PLASTICITY

Adaptive plasticity should evolve whenever individuals with the capacity to adjust their development to the prevailing conditions outperform, in the long run, individuals that express the same trait values or features constitutively, that is, regardless of condition. By “outperform” we mean “have a higher fitness,” that is, be more likely to survive or leave more offspring behind. The subtlety is in the phrase “in the long run.” In any single circumstance, the individual with the capacity to adjust its development to express the most suitable feature will perform just as well as the individual who expresses the same feature constitutively. But it will outperform all of the individuals who express unsuitable features constitutively. Individuals with the capacity to adjust development have high fitness in all conditions, whereas individuals with constitutive development patterns for the same set of features have high fitness in some conditions but low fitness in most conditions. In the long run, over many generations or many locations, individuals with the capacity to adjust development have the highest average fitness.

To illustrate the argument, consider the waterfleas that develop a thicker carapace in response to the presence of a predatory fly larva. Developing a thicker carapace takes energy that would be used otherwise to accelerate maturation and reproduction. When predators are present, the thicker carapace repays the investment because it reduces the ability of the fly larva to capture and kill the animal before it reproduces. In the absence of the predator, the thicker carapace is a waste of energy because it detracts from the ability of the waterflea to get on with the business of maturing, mating, and reproducing. A waterflea that made a thin carapace regardless of conditions would do well in the absence of predators but poorly in their presence; conversely, a waterflea that made a thick carapace regardless of conditions would thrive in the presence of predators but do poorly in their absence. The waterflea with the plastic developmental system has the best of both worlds and, if predators are present at some times but not others, would, in the long run, have a higher average fitness than waterfleas that develop thick or thin carapaces constitutively.

If plasticity is such an obvious advantage over constitutive development, why would developmental systems be anything but plastic when different features are suited to different conditions? The apparently

transparent advantage of phenotypic plasticity, as illustrated by the waterflea example, is based on three assumptions. The first assumption is that a reliable cue exists to inform the developing waterflea about the risk of predation from fly larvae. The second assumption is that there is no cost to plasticity; that is, the plastic developmental system produces a waterflea as fit as the constitutively thick carapace in the presence of fly larvae and as fit as the constitutively thin carapace in the absence of fly larvae. The third assumption is that each of the two conditions, presence or absence of flies, occurs with sufficient frequency that each constitutive development pattern often has the worse fitness.

Clearly, adaptive plasticity cannot evolve if the assumptions are blatantly false. For example, if there were no cue about the presence of predators, then there is no way to ensure the morphology appropriate for the condition, and the waterflea may as well guess which morphology to express. But what if we relax but do not void the assumptions? Suppose that a cue exists but is not perfectly reliable. Suppose that there is a fitness cost to plasticity; that is, the plastic system makes a slightly thinner carapace in the presence of the predator than does the unconditional “thick” system (and so is not quite as fit as “thick” when flies are present) and a slightly thicker carapace in the absence of the predator than does the unconditional “thin” system (and so is not quite as fit as “thin” when flies are absent). And suppose that the two conditions, presence or absence of predatory fly larvae, do not occur with equal frequency.

Now the prospects for the evolution of adaptive plasticity depend on complicated relationships among the reliability of the cue, the cost of plasticity, and the evenness in frequency of the two conditions. The waterflea example can illustrate this complexity. Consider what happens when only one condition is very common; perhaps predatory fly larvae are almost always abundant. In this case, the individuals expressing the thick carapace are likely to prevail because they are the fittest individuals nearly all of the time. For plasticity to persist, individuals carrying the plastic developmental system must have a tremendous fitness advantage over the individuals expressing thick carapaces constitutively when predatory flies are absent in order to make up for their comparative deficiency in fitness when flies are present. The greater the cost of plasticity when flies are present, and the more often flies are present, the greater the advantage the plastic waterfleas must have when flies are absent.

For a specific set of fitness relationships, the higher the variability in environmental circumstances, the more likely that plasticity in development will emerge

as a successful adaptation to that variability. However, this rule of thumb is valid only to a point. When conditions change too quickly, cues become unreliable, and plasticity does not improve on constitutive development or even random expression of features. This is especially true when plasticity is irreversible and the sensitivity to cues is restricted to a short period during development. If the environment changes faster than the time between the sensitive period and the expression of the appropriate feature, then plasticity is actually deleterious because it will perform worse than random expression of features.

Adaptive phenotypic plasticity enables individuals to cope with circumstances that vary from time to time and place to place but are not so variable as to preclude reliable cues to guide development. This enabling of individuals propagates upward to the level of the population and beyond to produce some important ecological consequences.

4. THE ECOLOGICAL IMPORTANCE OF PHENOTYPIC PLASTICITY

The obvious ecological consequence of phenotypic plasticity is that it allows a species to expand its range to seasonal environments and diverse habitats. A seasonal environment is the ideal situation for the evolution of plasticity; seasons change frequently enough to promote reversible plasticity but not too frequently compared to the time scale of trait expression, reliable cues abound, and many of the features of different seasons are predictable. Nearly everyone is familiar with the many adjustments that plants and animals make to the changes of season in temperate regions from the physiological changes underlying migratory behavior in birds to those underlying the onset of winter dormancy in trees.

Phenotypic plasticity can also allow species to occupy very uncertain habitats. Temporary ponds offer an example; the regular drying of the pond precludes sustainable fish populations, but the duration of the pond is uncertain, depending on the amount and timing of local rainfall. Nonetheless, temporary ponds harbor a considerable diversity of aquatic animals. Ponds offer refuge from what would otherwise be devastating predation by fish. But the dry periods would seem to preclude continuous occupancy by completely aquatic animals, and a short pond lifetime can leave the aquatic stage of animals that spend only part of their time in the water, such as tadpoles and dragonfly nymphs, high and dry if they cannot metamorphose quickly enough. Species that inhabit temporary ponds show remarkable varieties of phenotypic plasticity in response to drying conditions. Some copepods produce diapausing eggs

that rest in the soil, many of the frog and salamander larvae can accelerate their development as waters recede, and sirens (large, completely aquatic salamanders) burrow into the soil, secrete a waterproof cocoon around their bodies to prevent desiccation, and enter estivation until the waters return.

Habitats can also be uncertain in their biotic components, and plasticity in response to the risks of predation and parasitism enables a species to cope more effectively with varying levels of risk. Temporary ponds exemplify this situation as well. Not only is their duration uncertain, but so is the period between drying and refilling. When the pond refills soon after drying, it is colonized quickly by predaceous insects including dragonflies and backswimmers. The aquatic larvae can achieve very high densities by the time that tadpoles appear later in the season. But if the ponds are dry for a long time, tadpoles have little risk of predation because the insects are at very low densities and are very small in body size. Many tadpoles from temporary ponds display extensive phenotypic plasticity to the presence or absence of predators. Most species change their activity patterns to reduce their encounter rate with predators, and some species alter their tail coloration and morphology to avoid predator detection and escape predator attack.

But an example like this one raises an interesting question: if an organism evolves adaptive plasticity in response to variation in predation risk, does the advantage conferred by that plasticity have a reciprocal effect on the predator? This general question is at the heart of the close scrutiny that ecologists have been giving many examples of phenotypic plasticity. Indeed, reciprocal effects on predators or other biotic agents that induce plastic responses have been found in many studies and can ramify through a community and an ecosystem, with far-reaching consequences. To visualize this point, consider the tadpoles and dragonflies again. If the dragonflies are less able to procure tadpoles as food, they will increase their consumption of other prey such as aquatic invertebrates and cause their densities to decrease. Other predators in the system, which had been using aquatic invertebrates as their principal food resource, may then be forced into other trophic pathways. In effect, the adaptive plasticity in the tadpoles, once established, might drive a substantial change in species diversity, community structure, and perhaps even ecosystem processes such as nutrient cycling.

This kind of effect has been found in many cases, and the indirect effect of one species on another, mediated through the consequences of expressing a feature that is a response to a third species, is often called a *trait-mediated interaction*. In our example, the

decreased density of aquatic invertebrates represents an indirect effect of the tadpoles as they express the tail morphology that reduces their mortality rate from dragonfly predation. Trait-mediated interactions have been shown to be responsible for some interesting patterns of species diversity. For example, the presence of spiders in a New England old field causes several of their potential insect prey species to find refuge and foraging substrate on different plants than they would exploit in the absence of spiders. The plant preferred in the presence of spiders is actually a dominant competitor, and grazing by the insects reduces its density sufficiently for a competitively inferior species to increase in its density. The end result is that the presence of the spider increases the species diversity of the plant community.

A growing body of mathematical theory has elaborated on these basic ideas, indicating potentially profound effects of plasticity on species interactions. Much of this theory has been inspired by a particular type of adaptive plasticity, the inducible defenses of plants. *Induced defenses* are morphological or chemical responses by plants in response to herbivore attack. The production of toxic chemicals in some populations of wild parsnip in response to herbivore damage is an example of an induced chemical defense. Induced chemical defenses are known in a wide variety of plants, from freshwater algae to trees. Although the defensive compounds produced by plants can be synthesized and deployed relatively quickly, they can be costly to manufacture, diverting energy away from other functions. If the risk of herbivory is high, plants that produce them have higher fitness than those that do not; if the risk is low, chemical defense production is a waste of energy. Analogous to the argument for the carapace thickness of waterfleas, inducible defenses are favored when herbivory is sufficiently variable and a reliable cue is available (and being chewed is usually a reliable signal that herbivores are active).

Models inspired by inducible defenses indicate that adaptive plasticity can stabilize the numerical relationship between predator and prey or herbivore and host. To see this without mathematics, remember that predator-prey systems are inherently unstable because predators tend to overconsume prey. Any feature that protects a minimum fraction of the prey population from the predator can stabilize the system and allow predator and prey to coexist. Consider a herbivore-host system in which a constitutive defense appears via mutation. When this defense is expressed in some of the plants, it will protect a minimum fraction of individuals and stabilize the system. But as it spreads so that nearly all plants are protected, the herbivore loses its food resource and is likely to suffer a serious drop in

population size and perhaps even extinction. Now consider an inducible defense that is expressed only when the risk of herbivory is high. Initially, when the inducible defense is present in only a few plants, it stabilizes the interaction. As more individuals express the defense, the herbivores become food-limited, and their density starts to decrease. But as herbivore densities decrease, so does the risk of predation; fewer individuals will express the defense, leading to a greater opportunity for the herbivores, whose density can then increase. Eventually, the herbivore and plant populations reach equilibrium, and the proportion of plants expressing the defense also attains equilibrium. An experimental study of algae with and without inducible defenses has confirmed that inducible defenses can stabilize herbivore-host systems and even stabilize a system with three trophic levels: host, herbivore, and predator.

But theory shows that adaptive plasticity will stabilize a dynamic predator-prey or herbivore-host system only if prey respond to the cue—predation risk high or low—with just the right speed, compared to the rate at which predators or herbivores can change their consumption rate. Obviously, a response that is too slow will be ineffective at deterring predation. A response that is too fast introduces a time lag between the appearance of the defense and the effect on the predators that destabilizes the system. There are too many predators when prey are well defended and too few when they are not. Systems like this will start cycling in numbers to the point where either the prey or the predator becomes extinct. Whether rapid plastic responses actually destabilize species interactions is one of many empirical questions about adaptive plasticity that remain to be answered.

5. HORIZONS FOR FUTURE ECOLOGICAL RESEARCH ON PHENOTYPIC PLASTICITY

The most important of the longstanding unresolved issues is the cost of plasticity. This is a difficult problem. It is rare to find both constitutive and plastic expression of suitable features in one population, so it is usually not possible to make the appropriate comparisons of fitness. The most common experiments that attempt to measure the cost of plasticity compare families that differ in their levels of plasticity. The results have been equivocal; some experiments have detected apparent costs, but others have not. The tantalizing prospect of using genetic engineering to create constitutive expression offers considerable promise for resolving the magnitude of costs and whether those costs occur similarly in all environments.

The enthusiasm for studying trait-mediated interactions has produced an extensive documentation of

their existence and immediate effects. But in most cases, we do not know enough about the precision with which the traits are expressed, the relative frequencies of the different circumstances that provoke different expressions, or the full extent of the indirect effects that emerge in the community. We know that plasticity can have profound effects, but we do not know whether the documented cases of profound effects are exceptional.

Although we know a great deal about which factors induce plastic responses, we know far less about the actual cues that organisms exploit. Delineating those cues is important for illuminating their reliability, which is a critical feature governing plasticity's evolution and persistence. But there is another reason to identify the cues. Global change, *sensu lato*, could make erstwhile reliable cues unreliable, perhaps by dissociating combinations of signals that had been serving as very reliable cues. There is some evidence that this is happening in diapausing insects and migratory animals that use combinations of temperature and day length as their cue.

The mysteries of what we do not know about phenotypic plasticity should not detract from the marvel of what is well known. Through adaptive plasticity, an organism can remake itself, within limits, to suit its circumstances. And the organism that remakes itself to suit its circumstances can also remake the ecological circumstances around it, creating myriad possibilities for itself and for those who would understand the distribution and abundance of organisms.

FURTHER READING

- Bradshaw, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* 13: 115–155. *This article remains the single best essay on the entire subject. In this essay, Bradshaw describes phenotypic plasticity and distinguishes it from related ideas in the literature, tracing its intellectual history accurately from a letter of Charles Darwin in 1881 to the scientific literature of the early 1960s. Further, this article produced the technical terms still in use today, and Bradshaw's concluding section on research horizons helped determine the research on plasticity for several academic generations. Bradshaw cited a large number of examples, mostly but not entirely from plants, to support his claim that there were patterns in plasticity and that "plasticity is therefore a property specific to individual characters in relation to specific environmental influences." He discussed the types of variable environments in which one would expect to find plasticity, and his reasoning presaged the results of more sophisticated mathematical theory that would emerge over two decades later.*
- DeAngelis, D. L., M. Vos, W. M. Mooij, and P. A. Abrams. 2007. Feedback effects between the food chain and induced defense strategies. In N. Rooney, K. McCann, and D. Noakes, eds., *From Energetics to Ecosystems: The Dynamics and Structure of Ecological Systems*. New York: Springer Verlag, 213–236. *This report is among the most recent mathematical investigations of how inducible defenses can affect the stability of predator–prey or herbivore–host systems and, in a larger context, the responses of individual species and the ecosystem to nutrient enrichment. The discussion section of the article offers an excellent introduction to the literature on mathematical models of the consequences of plasticity for those interested either in further reading or, especially, initiating research on the subject.*
- DeWitt, T. J., and S. M. Scheiner, eds. 2003. *Phenotypic Plasticity: Functional and Conceptual Approaches*. New York: Oxford University Press. *This edited volume includes a broad range of papers that, together, cover every facet of the subject from the varieties of plasticity in nature to what we know (or knew in 2003) about the genetic control of plastic development. Readers who are considering initiating research in the broad area of phenotypic plasticity should use this volume as their road map to its current research horizons. A virtue of this collection is the significant number of essays by younger workers with fresh perspectives.*
- Karban, R., and I. T. Baldwin. 1997. *Induced Responses to Herbivory*. Chicago: University of Chicago Press. *This is a very readable monograph that reviews and synthesizes the literature on the varieties of inducible defenses in plants. The text brings theory, as it existed at the time, to bear on the diversity of ways in which plants respond to herbivory, and its wealth of examples still serves as a readable and effective introduction to the topic.*
- Kats, L. B., and L. M. Dill. 1998. The scent of death: Chemosensory assessment of predation risk by prey animals. *Ecoscience* 5: 361–394. *This is an underappreciated review paper that is focused on the diversity of chemical signals used by animals to assess predation risk and cue antipredator plasticity in a variety of traits. It is one of the few reviews in the ecological and evolutionary literature devoted primarily to a serious, thoughtful examination of specific cues and the all-important theoretical issue of their reliability.*
- Miner, B. G., S. E. Sultan, S. G. Morgan, D. K. Padilla, and R. A. Relyea. 2005. Ecological consequences of phenotypic plasticity. *Trends in Ecology and Evolution* 20: 685–692. *This short paper is one of the few review papers focused specifically on the ecological consequences of plasticity and argues for its importance as an ecological topic, not merely a topic in evolutionary biology. It is focused primarily on the effects of plasticity on species interactions and less on how plasticity enables habitat breadth. The paper and its bibliography offer an introduction to the recent literature on the various aspects of trait-mediated interactions and the effects of inducible defenses.*
- Pigliucci, M. 2001. *Phenotypic Plasticity: Beyond Nature and Nurture*. Baltimore, MD: The Johns Hopkins University Press. *This book is a recent synthesis of the evolution of plasticity, and Pigliucci's advocacy for thinking about integrated developmental systems is, in some ways, a modern counterpart to Schmalhausen's book. One of the*

- book's strengths is its treatment of modern theory for the evolution of plasticity; the text offers lucid explications of some very complicated ideas, many of which have their origins in sophisticated mathematical theory, and clarifies the relationships among different theoretical approaches and the results of individual papers. Readers interested in a comprehensive introduction to the theory for the evolution of plasticity should read the treatment in this book.
- Schmalhausen, I. I. 1949. *Factors of Evolution*. Philadelphia: The Blakiston Company. Reprinted Chicago: University of Chicago Press, 1986. *This classic monograph emphasizes the evolution of integrated development systems for organisms. Schmalhausen took a unified view of evolutionary development, placing plasticity in the same conceptual context as its opposite, canalization, which is the process of minimizing the variation in development so as to produce the same features or trait values regardless of environmental conditions. He discussed how and when evolution might take each course and set these ideas firmly in the context of what were, at that time, modern ideas in evolutionary genetics. The book still offers a compelling argument that developmental systems are adaptive evolution's most breathtaking product.*
- Shapiro, A. M. 1976. Seasonal polyphenism. *Evolutionary Biology* 9: 259–333. *This underappreciated review is a very thoughtful treatment of seasonal variation in morphology, coloration, and life history, with some close attention to insects. The text touches on the major themes in the evolution of plasticity and, despite its age, remains an excellent source of ideas and a laudable example of how to synthesize natural history, conceptual issues, and data.*
- Sumner, F. B. 1932. Genetic, distributional, and evolutionary studies of the subspecies of deer mice (*Peromyscus*). *Bibliographica Genetica* 9: 1–106. *This is a classic paper that summarizes and synthesizes Sumner's decades of study of deer mouse ecology, genetics, and development. Sumner took the integrated approach to ecology and evolution that is so often proclaimed but so rarely practiced. The paper discusses how local adaptation (genetic differences produced by Darwinian adaptation to local conditions) and phenotypic plasticity combine to allow deer mice to occupy diverse habitats. His experimental dissections of phenotypic variation into its genetic, environmental, and interactive components remain models for modern emulation.*
- Tollrian, R., and C. D. Harvell, eds. 1998. *The Ecology and Evolution of Inducible Defenses*. Princeton, NJ: Princeton University Press. *This volume offers a comprehensive look into its subject, and the papers included in the volume examine topics from the biochemistry of defensive compounds to trait-mediated interactions. Although the papers were written before the recent flowering of mathematical theory for the consequences of plasticity, the ideas that those theories examine are set out in several of these papers, and the volume clearly played a role in accelerating this area of research. For a reader interested in the variety of induced defenses, this volume offers a strong introduction to a very diverse literature. In addition, the authors of individual papers come from several schools of thought, and therefore the volume offers varied perspectives on its topic that some other edited volumes do not.*
- Travis, J. 1994. Evaluating the adaptive role of morphological plasticity. In P. C. Wainwright and S. M. Reilly, eds., *Ecological Morphology: Integrative Organismal Biology*. Chicago: University of Chicago Press, 99–122. *This review paper was written for the scientist who is not a specialist in evolutionary biology or ecology and wishes to learn about phenotypic plasticity. It offers a synthetic examination of phenotypic plasticity, reviewing the conclusions of mathematical theory—but without the mathematics—for its evolution and matching a large number of examples, primarily drawn from animals, to the classes of theoretical treatments to which those examples apply. Although theory has advanced considerably since it was written, it is still a lucid introduction to the literature, especially the terminology, and its strength is in describing clear patterns in the vast array of examples.*

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