Genetic Variation and Evolution

We have already discussed other examples of genetic variation. We have looked at genetic variation among HIV virions in their susceptibility to the antiretroviral drug AZT as well as genetic variation among humans in the susceptibility to HIV infection. We have considered genetic variation among sticklebacks in the extent of body armor and genetic variation in fruit size in tomatoes. We will see many more examples throughout the book.

We have also discussed the role of genetic variation in evolution. Because genes are passed from parents to offspring, genetic variants associated with higher survival and reproductive success automatically become more common in populations over time, while variants associated with untimely death and reproductive failure disappear. Genetic variation is the raw material for evolution.

But there is more to the story of variation and evolution. That is why we now turn to environmental variation.

Environmental Variation

Our example of environmental variation concerns a prey species, the water flea, and its predator, a larval insect. The fossil record shows that phantom midges have been eating water fleas for 145 million years (Kotov and Taylor 2011).

Water fleas are tiny freshwater crustaceans that inhabit lakes and ponds all over the world (Lampert 2011). Among the traits that make water fleas useful for the study of environmental variation is that when conditions are auspicious they reproduce by cloning, switching to sexual reproduction only when conditions deteriorate. Also useful is that certain environmental cues trigger changes in their morphology, physiology, and behavior. Together these characteristics make it possible for researchers to expose genetically identical water fleas to different cues and get a pure look at how changes in the environment influence phenotype.

The water flea *Daphnia pulex* suffers substantial predation by phantom midge larvae, but only at certain times and places. *Daphnia pulex* is capable of developing a morphology that is well defended against phantom midges **(Figure 5.8a)**. It can nearly double the strength and thickness of its carapace and grow ridges, called neckteeth, on the back of its head (Laforsch et al. 2004). These defenses are costly, however (Hammill et al. 2008). Apparently as a result, *D. pulex* has evolved the capacity to grow anti-midge armor only when it smells midges. The water fleas in Figure 5.8 look different not because they carry different genes, but because they have been exposed to different chemical environments.

The chemical the water flea can detect emanating from phantom midges remains to be identified. Biologists refer to it by the generic term *kairomone*. *Daphnia pulex*'s growth of armor in response to phantom midge kairomone is an example of an **inducible defense**.

Hitoshi Miyakawa and colleagues (2010) suspected that to grow anti-midge armor, a water flea has to boost its production of a variety of proteins involved in development. The researchers exposed *Daphnia pulex* to kairomone from the phantom midge *Chaoborus flavicans* and compared them to genetically identical unexposed individuals. The researchers looked at the production, or **expression**, of dozens of candidate proteins they had reason to think, from earlier research, might play a role in *Daphnia*'s inducible defenses. They measured protein production indirectly, by quantifying the production of messenger RNA, the molecular intermediary that carries genetic information from the DNA in the nucleus to the ribosomes in the cytoplasm where proteins are built.

Environmental variation consists of differences among individuals due to exposure to different environments. One way environments can influence phenotype is by altering gene expression.

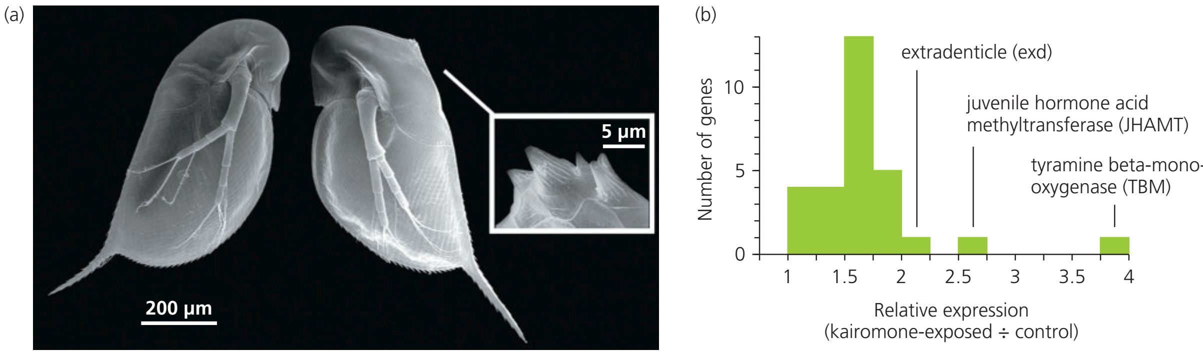

Figure 5.8 Inducible defenses in *Daphnia* (a) Juveniles that smell phantom midge larvae grow neck teeth and other defenses. Photo by Christian Laforsch. (b) This involves boosting production of many proteins. From data in Miyakawa et al. (2010).

The graph in Figure 5.8b shows the expression of 29 candidate genes in kairomone-exposed *D. pulex* relative to their expression in unexposed individuals. In every case, the exposed water fleas made more messenger RNA and thus presumably more protein. The proteins with the largest increase in expression upon exposure to kairomone were extradenticle (exd), juvenile hormone acid methyltransferase (JHAMT), and tyramine beta-monooxygenase (TBM). Exd acts during development to influence the identity of appendages in arthropods. JHAMT is an enzyme required for the synthesis of juvenile hormone, a major regulator of arthropod development. TBM is an enzyme that catalyzes the synthesis of neurotransmitters, chemicals used by nerve cells to send messages to each other.

Many details remain to be discovered, but Miyakawa's results show that the mechanism by which *D. pulex* changes its phenotype when it smells phantom midges involves changes in the production of a variety of proteins.

Environmental Variation and Evolution

Many other organisms alter the identity or quantity of the proteins they make in response to changes in the environment, thereby altering their phenotype. Human athletes living at low altitude, but training at simulated high altitude, produce more vascular endothelial growth factor (VEGF) than athletes living and training at low altitude (Hoppeler and Vogt 2001). The extra VEGF stimulates the growth of capillaries in the muscles. Environmental variation is ubiquitous.

The non-genetic influences on protein expression, and thus phenotype, even include chance. The *Escherichia coli* bacteria in Figure 5.9 are genetically identical. Michael Elowitz and colleagues (2002) inserted into the DNA of their common ancestor two copies of the gene for green fluorescent protein (GFP). The two copies encode distinct variants of GFP that emit different colors of light when they fluoresce. They are controlled by identical promoters—the switches that turn genes on or off. A bacterium making equal amounts of both versions of GFP would be yellow, a cell making more of one version would be green, and a cell making more of the other version would be orange. The explanation for the diversity of colors in the photo is random variation in the interactions between the promoters and the regulatory proteins that activate and deactivate them.

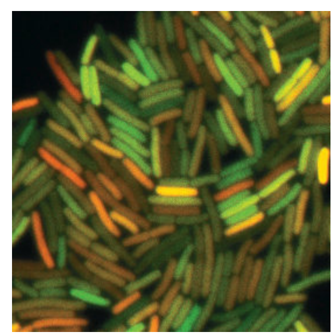

Figure 5.9 Random variation in protein production in genetically identical bacteria These cells are different colors because they are making different amounts of two fluorescent proteins. From Elowitz et al. (2002).

Despite its ubiquity, environmental variation supplies no raw material for evolution. This is because environmentally induced changes in phenotype are not transmitted to future generations. Whether a water flea born by clonal reproduction has neckteeth is determined not by the genes she inherits, but by the