SECTION III *Population Ecology*



Chinese proverb

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Population Genetics and Natural Selection

Chapter

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arwin's theory of evolution by natural selection, the unifying concept of modern biology, was crystallized by his observations in the Galápagos Islands. In mid October of 1835 under a bright equatorial sun, a small boat moved slowly from the shore of a volcanic island to a waiting ship. The boat carried a young naturalist who had just completed a month of exploring the group of islands known as the Galápagos, which lie on the equator approximately 1,000 km west of the South American mainland (fig. 8.1). As the seamen rowed into the oncoming waves, the naturalist, Charles Darwin, mused over what he had found on the island. His observations had confirmed expectations built on information gathered earlier on the other islands he had visited in the archipelago. Later Darwin recorded his thoughts in his journal which he later published (Darwin 1839), "The distribution of the tenants of this archipelago would not be nearly so wonderful, if, for instance, one island had a mockingthrush, and a second island some other quite distinct genusif one island had its genus of lizard and a second island another distinct genus, or none whatever. . . . But it is the circumstance, that several of the islands possess their own species of the tortoise, mocking-thrush, finches, and numerous plants, these species having the same general habits, occupying analogous situations, and obviously filling the same place in the natural economy of this archipelago, that strikes me with wonder [emphasis added].

Darwin wondered at the sources of the differences among clearly related populations and attempted to explain the origin of these differences. He would later conclude that these populations were descended from common ancestors whose descendants had changed after reaching each of the islands. The ship to which the seamen rowed was the H.M.S. Beagle, halfway through a voyage around the world. The main objective of the Beagle's mission, charting the coasts of southern South America would be largely forgotten, while the thoughts of the young Charles Darwin would eventually develop into one of the most significant theories in the history of science. Darwin's wondering, carefully organized and supported by a lifetime of observation, would become the theory of evolution by natural selection, a theory that would transform the prevailing scientific view of life on earth and rebuild the foundations of biology.

Darwin left the Galápagos Islands convinced that the various populations on the islands were gradually modified from their ancestral forms. In other words, Darwin concluded that the island populations had undergone a process of **evolution**, a process that changes populations of organisms over time. Though Darwin left the Galápagos convinced that the island populations had evolved, he had no mechanism to explain the evolutionary changes that he was convinced they had undergone. However, a plausible mechanism to produce evolutionary change in populations came to Darwin almost exactly 3 years after his taking leave of the Galápagos Islands. In October of 1838 while reading the essay on populations by Thomas Malthus, Darwin was convinced that during competition for limited resources, such as food or space, among individuals



Figure 8.1 On the Galápagos Islands Charles Darwin encountered many examples of readily observed plants and animal species that differed physically from one island to another island. Here a Galápagos hawk lands on a giant tortoise for which the islands are named.

within populations, some individuals would have a competitive advantage. He proposed that the characteristics producing that advantage would be "preserved" and the unfavorable characteristics of other individuals would be "destroyed." As a consequence of this process of selection by the environment, populations would change over time. With this mechanism for change in hand, Darwin sketched out the first draft of his theory of natural selection in 1842. However, it would take him many years and many drafts before he honed the theory to its final form and amassed sufficient supporting information. Darwin's theory of natural selection can be summarized as follows:

- 1. Organisms beget like organisms. (Offspring appear, behave, function, and so forth like their parents.)
- 2. There are chance variations between individuals in a species. Some variations (differences among parents) are heritable (are passed on to offspring).
- 3. More offspring are produced each generation than can be supported by the environment.
- 4. Some individuals, because of their physical or behavioral traits, have a higher chance of surviving and reproducing than other individuals in the same population.

Darwin (1859) proposed that differential survival and reproduction of individuals would produce changes in species populations over time. That is, the environment acting on variation among individuals in populations would result in **adaptation** of the population to the environment. He now had a mechanism to explain the differences among populations that he had observed on the Galápagos Islands. Still, Darwin was keenly aware of a major insufficiency in his theory. The theory of natural selection depended upon the passage of "advantageous" characteristics from one generation to the next. The problem was that the mechanisms of inheritance were unknown in Darwin's time. In addition, the prevailing idea at the time, blending inheritance, suggested that rare traits, no matter how favorable, would be blended out of a population, preventing change as a consequence. Darwin worked for nearly half a century to uncover the laws of inheritance. However, he did not. To do so required a facility with mathematics that Darwin had not developed. In a short autobiography, Darwin himself (1859) remarked, "I attempted mathematics, and even went during the summer of 1828 with a private tutor . . . but I got on very slowly. The work was repugnant to me, chiefly from my not being able to see any meaning in the early steps in algebra. This impatience was very foolish, and in after years I have deeply regretted that I did not proceed far enough at least to understand something of the great leading principles of mathematics, *for men thus endowed seem to have an extra sense*" [emphasis added].

As Darwin explored the Galápagos Islands, halfway around the world in central Europe a schoolboy named Johann Mendel was studying under difficult conditions and developing the facility with mathematics necessary to complete Darwin's theory of natural selection. At thirteen, Johann was half Darwin's age, yet he had already set a course for a life of study which he followed as resolutely as the crew of the *Beagle* on their voyage around the world. At the end of his scientific voyage, Mendel would uncover the basic mechanisms of inheritance.

Mendel was the oldest child of a family that farmed a small landholding near Brno, a town in what is now the Czech Republic. He would have had little schooling if it were not for the philanthropy of the countess Walpurga Truchsess-Zeil who ruled the district in which Mendel's family lived. The countess had a standing order to her advisors that they should identify all of the promising boys and girls living within her domain and send them to school, where she paid their room and board. Mendel had been one of those children. The countess was more than a philanthropist, however. She also paid attention to details, including the curriculum of her school, which she specified should include the natural sciences. Thus from the outset, Mendel's studies included a firm grounding in the sciences. A countess with foresight, intelligence, and heart and her perceptive advisors had discovered an intellectual treasure and provided for the blossoming of one of biology's great geniuses.

Johann would be renamed Gregor Mendel when he joined the Augustinian order of monks that maintained a monastery near his birthplace. In a garden within the walls of the abbey, Mendel would discover what Darwin's around-theworld voyage would not reveal. The two keys to Mendel's discoveries would be excellent training in mathematics and physics from which he derived a sense of quantitative relationships and the power of experimental approaches to the study of the natural world.

What did Mendel discover? Briefly he discovered what we now call "Mendelian genetics," including the very fundamental concept of particulate inheritance. That is the concept that characteristics pass from parent to offspring in the form of discrete packets of information that we now call genes. Mendel also determined that genes come in alternative forms, which we term **alleles.** For instance, Mendel worked with alleles such as round versus wrinkled seeds and tall versus short plants. In addition, he found that some alleles prevent



Figure 8.2 Garden pea plant in flower. Because the garden pea normally self-pollinates, Mendel could keep track of and control mating in his study plants.

the expression of other alleles. We call such alleles "dominant" and the alleles that they suppress "recessive." Mendel's work also revealed the distinction between genotype and phenotype and the difference between homozygous and heterozygous genotypes. Mendel's work, which revealed still other aspects of the laws of inheritance, laid a solid foundation for the science of genetics.

How did Mendel succeed, while so many others had failed? The sources of his success can be traced to his education and his own special genius. Mendel's education at the University of Vienna exposed him to some of the best minds working in the physical sciences and to an approach to science that emphasized experimentation. His introduction to the physical sciences included a solid foundation in mathematics, including probability and statistics. As a consequence, Mendel could quantify the results of his experimental research.

Mendel chose to work with plants which could be maintained in the abbey garden. His most famous and influential work was done on the garden pea, *Pisum sativum*, that has many desirable traits (fig. 8.2). Many domestic varieties of peas, which showed a great deal of physical variation, with its attendant underlying genetic variation, were available to Mendel. However, he subjected the phenotypes of his study organisms to careful analysis. Rather than treat the phenotype as a whole, Mendel subdivided the organism into a set of manageable characteristics such as seed form, stem length, and so forth, which it turned out were controlled by individual genes. This analytical perspective of his study organisms was probably another legacy of his training in the physical sciences. Finally, to his excellent education and genius, Mendel added a lot of hard work and perseverance. For a full

discussion of Mendel, his work and its ongoing analysis, including controversial aspects of the work, see the excellent biography by Orel (1996).

Darwin and Mendel complemented each other perfectly and their twin visions of the natural world revolutionized biology. The synthesis of the theory of natural selection and genetics gave rise to modern evolutionary ecology, a very broad field of study. Here we examine five major concepts within that broad discipline.



- Phenotypic variation among individuals in a population results from the combined effects of genes and environment.
- The Hardy-Weinberg equilibrium model helps identify evolutionary forces that can change gene frequencies in populations.
- Natural selection is the result of differences in survival and reproduction among phenotypes.
- The extent to which phenotypic variation is due to genetic variation determines the potential for evolution by natural selection.
- Random processes, such as genetic drift, can change gene frequencies in populations, especially in small populations.

CONCEPT DISCUSSION

Variation Within Populations

Phenotypic variation among individuals in a population results from the combined effects of genes and environment.

Because phenotypic variation is the substrate upon which the environment acts during the process of natural selection, determining the extent and sources of variation within populations is one of the most fundamental considerations in evolutionary studies. The following examples review variation in representative plant and animal populations and some of the early methods used to uncover that variation.

Variation in Plant Populations

Darwin's theory of natural selection sparked a revolution in thinking among biologists, who responded almost immediately by studying variation among organisms in all sorts of



Figure 8.3 *Potentilla glandulosa*, sticky cinquefoil, grows from sea level to over 3,000 m elevation and shows remarkable morphological variation along this elevational gradient.

environments. The first of these biologists to conduct truly thorough studies of variation and to incorporate experimentation in their studies, focused on plants.

Phenotypic and Genetic Variation in Potentilla glandulosa

Jens Clausen, David Keck, and William Hiesey, who worked at Stanford University in California, conducted some of the most widely cited studies of plant variations. Their studies provided deep insights into the extent and sources of morphological variation in plant populations, including both the influence of environment and genetics. Though this research group and its successors studied nearly 200 species, it is best known for its work on *Potentilla glandulosa* or sticky cinquefoil (fig. 8.3) (Clausen, Keck, and Hiesey 1940).

Clausen and his research team worked with clones of several populations of *P. glandulosa*, which they grew in three main experimental gardens—one at Stanford near the coast at an elevation of 30 m, another in a montane environment at Mather at an elevation of 1,400 m in the Sierra Nevada, and a third garden in an alpine environment at Timberline at 3,050 m. By cloning lowland, mid-elevation, and alpine plants and growing them in experimental gardens, Clausen, Keck, and Hiesey established experimental condi-

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Figure 8.4 Growth responses by *Potentilla glandulosa* grown at three elevations (data from Clausen, Keck, and Hiesey 1940).

tions that could reveal potential genetic differences among populations. In addition, because they studied the responses of plants from all populations to environmental conditions in lowland, mid-elevation, and alpine gardens, their experiment could demonstrate adaptation by *P. glandulosa* populations to local environmental conditions.

Two responses of *P. glandulosa* to environmental conditions at the three common garden sites are summarized in figure 8.4. Plant height differed significantly among the study sites, which shows an environmental effect on plant morphology, but the lowland, mid-elevation and alpine plants responded differently to the three environments. For instance, while the mid-elevation and alpine plants attained their greatest height in the mid-elevation garden, the lowland plants grew the tallest in the lowland garden. In the gardens corresponding to their natural elevation, the mid-elevation and alpine plants produced more flowers than the other two ecotypes. The lowland ecotype, in contrast, did not produce the most flowers in any of the experimental gardens. These differences in response by different ecotypes indicate genetic differences among populations of *P. glandulosa*.

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Other information indicates that genetic differences among the plants are associated with adaptation to the environments of the native elevation. It is clear that lowland ecotypes of P. glandulosa are excluded from the alpine. Most died during their first winter in the alpine garden and those that survived flowered during the following summer but their fruits did not mature. Mid-elevation P. glandulosa also survived poorly in the alpine and their fruits often failed to mature. Alpine plants showed the opposite trends. They had poor survival in the lowland garden and went dormant in winter, while the lowland plants remained active. In summary, the experiments of Clausen, Keck, and Hiesey demonstrated genetic differences among populations and adaptation to their natural environments. Ecologists call such locally adapted and genetically distinctive populations within a species ecotypes. Applying this term then, we can conclude that the lowland, mid-elevation, and alpine populations studied by Clausen, Keck, and Hiesey were ecotypes. Using transplant and common garden approaches ecologists have learned a great deal about genetic variation among and within plant populations. These classical approaches combined with modern molecular techniques are rapidly increasing our knowledge of genetic variation in natural populations.

Combining Molecular and Morphological Information

In the previous classic example, Clausen, Keck, and Hiesey used differences in growth form of *P. glandulosa* plants grown in common gardens to infer genetic differences among populations of this species. More recently, Kjell Hansen, Reidar Elven, and Christian Brochmann combined molecular and morphological techniques to explore genetic variation in populations of *Potentilla* species living on Spitsbergen Island in the high Arctic. Spitsbergen is the largest island in the Svalbard archipelago, a far northern part of the country of Norway (fig. 8.5).

Hansen, Elven, and Brochmann (2000) were interested in whether a combination of genetic and morphological information could help them understand the complex variation of the type seen in *Potentilla* species (see fig. 8.4). One of the questions addressed by this team from the Botanical Garden and Museum of the University of Oslo, Norway concerned a group of forms known as the Potentilla nivea complex. Based on morphological evidence, the complex had been divided into three species: P. chamissonis, P. insularis, and P. nivea. A second problem addressed by the researchers was whether three distinctive forms of P. pulchella should be recognized as different taxa, perhaps varieties or subspecies, within P. pulchella. The typical form of P. pulchella is large and hairy and grows in a variety of habitats, including cliffs, in cliff meadows where seabirds deposit significant quantities of feces, and on ridges. A second form of P. pulchella, which is small and lacks abundant hairs, grows on gravel terraces along shorelines. The third form is small and hairy and grows on silty shoreline terraces.



Figure 8.5 High above the Arctic Circle, the island of Spitzbergen presents an extreme environment for terrestrial plants.

Hansen, Elven, and Brochmann sampled 17 populations of *Potentilla*. The area on Spitsbergen where Hansen, Elven, and Brochmann collected *Potentilla* extended from about 78° to over 79° N latitude. Ten of these populations were of the *P. nivea* complex and seven were populations of *P. pulchella*. Using these collections, Hansen, Elven, and Brochmann studied 64 morphological characters of 146 plants and they did genetic analyses of 136 plants. Genetic analyses were done using the randomly amplified polymorphic DNA, or RAPD, method (see Applications & Tools). Again, the question addressed by the researchers was whether genetic information combined with morphology would support the earlier recognition of three species within the *P. nivea* complex and the subdivision of *P. pulchella* into three different taxa.

The results of this study demonstrate the utility of joining morphological information with genetic information. The RAPD method identified three genetically distinct groups of plants within the *P. nivea* complex, which we can call "RAPD phenotypes." Significantly, most of the genetic variance within the *P. nivea* complex was due to variation between the proposed species, while much less was due to variation within each of the proposed species (fig. 8.6). The three RAPD phenotypes were also separated clearly on the basis of several morphological characters. It turned out that the separation of plants achieved by Hansen, Elven, and Brochmann, which was based on combined genetic and morphological data, corresponded precisely to the three previously proposed species: *P. chamissonis, P. insularis,* and *P. nivea.* These results support the continued recognition of these taxa.

In contrast, the results of the study did not support recognizing the three morphologically distinctive forms of *P. pulchella* as separate taxa. Despite their substantial morphologi-



Figure 8.6 Sources of genetic variance between and among proposed species within the *Potentilla nivea* complex.

cal differences, the most common RAPD phenotype was observed in all three forms of *P. pulchella*. From this result, Hansen, Elven, and Brochmann concluded that the morphologically distinctive forms in *P. pulchella* result from plastic growth responses to local environments or perhaps are due to the effects of a small number of genes. As a consequence, the researchers concluded that the three forms of *P. pulchella* should not be recognized as separate taxa.

The ability of researchers to study the genes of organisms directly has revolutionized evolutionary and ecological studies. However, the older experimental garden approaches remain essential for answering some types of scientific questions, particularly in studies of plants. As the following example shows, however, these approaches have also been used successfully by ecologists studying animal populations.

Variation in Animal Populations

Studies of phenotypic and genetic variation among animal populations are usually more difficult than similar studies of plant populations. However, the chuckwalla, *Sauromalus obesus*, a large herbivorous lizard of the southwestern United States and northwestern Mexico (fig. 8.7) has been studied almost as thoroughly as some of the plant species just discussed. *Sauromalus* prefers to feed on annual forbs and grasses but will feed on the leaves of shrubs if its preferred and more nutritious foods are not available. Though it grows most rapidly when young, the species continues growing throughout life, reaching a body length of over 220 mm (excluding the tail) and a mass of about 400 g.

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Figure 8.7 A chuckwalla, *Sauromalus obesus*. Chuckwallas are large herbivorous lizards living in the southwestern United States and northwestern Mexico.

Ted Case (1976) explored variation in body size among *Sauromalus* populations at twelve sites distributed across its geographic range. Because the environments in which *Sauromalus* lives vary greatly across its range, we might expect that environmental selection has favored different characteristics in different parts of the species range. Case found that average summer temperatures at his desert study sites ranged from 23.8° to 35°C, while average annual rainfall varied from approximately 35 to 194 mm.

Clearly, *Sauromalus* lives in hot, dry places. Just how hot and dry some of these places are is shown by the climate graph for one of Case's study sites, Yuma, Arizona (see fig. 2.19). However, Case found considerable variation in climate over the elevational range of 4 to 1,166 m where *Sauromalus* lives. Elevation was especially well correlated with winter weather (fig. 8.8). As you can see in figure 8.8, average winter rainfall increases with elevation, from less than 20 mm at the lowest elevations to over 60 mm at the highest elevations. Winter rain is critical for growing the annual herbaceous plants which *Sauromalus* prefers to eat and the amount of winter rainfall largely determines the amount of plant growth in these desert environments.

Higher average rainfall at higher elevations translates into more food available for *Sauromalus*. However, the higher elevations inhabited by *Sauromalus* not only receive higher average rainfall, they also show less year-to-year variation in amount of rainfall. At the other end of the environmental spectrum, the *Sauromalus* at lower elevations lives in environments where much less rain falls and where there is more year-to-year variation in rainfall. What does variation in rainfall mean to *Sauromalus*? Variation in rainfall translates into variation in food availability. The lizards at lower elevations, on average, have access to less food and the amount available on any given year is unpredictable. Meanwhile the lizards at higher elevations live in a relatively food-rich environment where food availability is much more constant.



Figure 8.8 Average winter rainfall and variation in rainfall among sites inhabited by *Suromalus obesus* (data from Case 1976).



Figure 8.9 Relationship between winter rainfall and chuckwalla, *Sauromalus*, size (data from Case 1976).

Case found that the lizards from the food-rich higher elevations are approximately 25% longer than those from lower elevations. This difference in body length translates into a twofold difference in body weight! What is the source of these size differences among populations? Of the many environmental variables that he measured, Case determined that the best predictor of *Sauromalus* body length across his study sites is average winter rainfall (fig. 8.9).

Case uncovered substantial variation in size among *Sauromalus* populations. This variation is analogous to the variation in plant sizes observed by plant ecologists along elevational gradients. How might we determine whether the

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differences in body size among *Sauromalus* populations Case observed are due to differences in food availability or due to genetic differences among populations? Like the plant ecologists Clausen, Keck, and Hiesey, we could rear individuals from low- and high-elevation populations in a common environment. That is, we could construct a kind of common garden for lizards. This is precisely what was done by Christopher R. Tracy (1999).

Tracy collected 12 to 15 juvenile *Sauromalus* from six populations in Arizona, California, and Nevada, living at elevations ranging from 200 to 890 m. He then raised these juvenile lizards under identical environmental conditions in a laboratory. By growing juvenile *Sauromalus* under identical environmental conditions, Tracy could determine the contributions of environmental versus genetic factors to size differences among *Sauromalus* populations.

Tracy set up the laboratory environment in a way that simulated late spring conditions, including 14 hours of light and 10 hours of darkness daily. These conditions provided the lizards with long periods for daily activity. He provided rocks for shelter and a heat lamp for basking. The laboratory environment maintained a temperature gradient from room temperature to 42°C under a heat lamp, which allowed the lizards the opportunity to use behavior to maintain their body temperatures at a preferred 36°C. Tracy also made an abundance of high quality food and vitamins available at all times so that food would not limit rates of lizard growth. In addition, he took Sauromalus social life into account. Observations by other ecologists had shown that Sauromalus eats more and grows faster when living in small groups than when isolated from other Sauromalus. Therefore, Tracy kept his lizards in groups of 3 to 5 while he followed their growth under laboratory conditions for 462 days.

How did *Sauromalus* from different elevations respond to Tracy's laboratory conditions? Lizards from all populations grew well in the laboratory. However, they showed marked different patterns of growth. First, females grew slower than males but individuals of both sexes grew faster before reaching sexual maturity. However, before sexual maturity, the fastest growth was shown by lizards from low elevations. After maturity, however, the lizards from higher elevations grew faster. Despite these complications the outcome of the experiment was clear. Lizard size at the end of the laboratory experiment was highly and positively correlated with the elevation at which they had been collected as juveniles (Fig. 8.10). In the end lizards from the higher elevations grew to a larger size, approximating in a laboratory common garden for lizards the pattern of variation in body size found in the field.

What do the results of Tracy's experiment indicate about variation in body size among *Sauromalus* populations? One important conclusion is that the differences in body size observed in the field are at least partly determined by genetic differences among populations. It appears that natural selection has favored different sized individuals at different elevations. Tracy's study of *Sauromalus* demonstrates how traditional morphological and laboratory studies continue to make



Figure 8.10 Chuckwalla body lengths at the end of a laboratory rearing experiment (data from Tracy 1999).

significant contributions to our understanding of variation in animal populations. However, modern molecular approaches dominate contemporary studies of genetic variation in animal populations. The following study shows how molecular studies of genetic variation may be combined with morphological studies to explore the distribution and extent of genetic variation in animal populations, even where the historical patterns have been obscured by human interference.

Genetic Variation in Alpine Fish Populations

The Alps rise out of the landscape of south central Europe, forming a moist and cool high-elevation environment. The Alps' deep winter snows and glaciers make them the origin of four important rivers: the Danube and Rhine Rivers, which flow out of the northern Alps, and the Po and Rhone Rivers, which flow out of the southern Alps. Because the headwater streams of these rivers are cool, they became refuges for coldwater aquatic organisms following the last Ice Age. As temperatures of the surrounding lowlands began to warm at the end of the Pleistocene, approximately 12,000 years ago, aquatic species requiring cold water migrated to the headwaters of these rivers. The movement of cold-adapted aquatic species into the headwater streams and lakes of the glacial valleys that lace the Alps created clusters of geographically isolated populations. This isolation reduced movements of individuals between populations. With reduced gene flow, populations could diverge genetically. Such genetic divergence would increase the genetic variation among populations.

Morphological differences among populations of headwater fish species in the Alps have long suggested genetic differences among them. Nowhere has morphological variation among pop-

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ulations been better studied and documented than among the whitefishes. Whitefish are relatives of the trout and salmon and are classified in the genus *Coregonus* (fig. 8.11). Marlis Douglas and Patrick Brunner (2002) explored the genetic and phenotypic variation among populations of *Coregonus* in the central Alps. Douglas and Brunner pointed out that ichthyologists have described 19 indigenous *Coregonus* populations from the central Alps. However, there has been significant disagreement over the taxonomic status of these 19 populations. The classification of these populations ranges from that of a single variable species with 19 distinctive populations to dividing the 19 populations into more than a dozen separate species.

The taxonomic status of *Coregonus* populations in the central Alps is made more difficult by a one-hundred-year history of intensive fisheries management. Douglas and Brunner review this history, which included raising *Coregonus* in hatcheries and moving fish between lakes. One of the main purposes of the study by Douglas and Brunner was to describe the genetic variation among the present-day populations of *Coregonus* in order to determine if there is evidence for significant genetic differences among historically recognized populations. A second purpose was to examine the genetic similarity between introduced *Coregonus* populations and the populations from which they were drawn. Using this information, Douglas and Brunner intended to offer suggestions for the management and conservation of *Coregonus* in the central Alps.

Douglas and Brunner collected 907 *Coregonus* specimens from 33 populations in 17 lakes in the Central Alpine Region of Europe. They used a mixture of anatomical and genetic features to characterize the fish collected from the study populations. The anatomical features were the number of rays in the dorsal, anal, pelvic, and pectoral fins, the extent of pigmentation in these fins, and the number of gill rakers on the first gill arch. The study populations were characterized genetically by using specific primers to amplify six different loci on **microsatellite DNA**, tandemly repetitive nuclear DNA, 10–100 base pairs long.

Genetic analyses by Douglas and Brunner demonstrated a moderate to high level of genetic variation within all 33 study populations. They also found that genetic and morphological analyses distinguished the 19 historically recognized Coregonus populations of the central Alps. Genotypic differences among populations were sufficient to correctly assign individual fish to the indigenous population from which they were sampled with approximately a 71% probability. Fin ray counts correctly assigned fish to the 19 indigenous populations with a 69% probability, while pigmentation could identify them with a 43% probability. Combining genetic and phenotypic data increased the correct assignment of specimens to the populations from which they were drawn to 79%. Genetic analyses of the introduced Coregonus populations revealed their genetic similarity to the populations from which they were stocked. However, these analyses also showed that the introduced populations have become genetically distinctive from their source populations.

The conclusion that Douglas and Brunner drew from these results was that the *Coregonus* of the central Alps is made up of a highly diverse set of populations that show a high level of genetic



Figure 8.11 Whitefish, *Coregonus* sp., are adapted to cold, highly oxygenated waters like their relatives the trout and salmon. Because they are valued food fishes, whitefish have been intensively managed particularly in the central Alps.

differentiation. They suggest that these populations should be considered as an "evolutionarily significant unit." They further conclude that the distinctiveness of local *Coregonus* populations is sufficient so that they should be managed as separate units. Douglas and Brunner recommend that *Coregonus* should not be moved from one lake basin to another.

The studies of plants and animals that we have reviewed have repeatedly demonstrated genetic variation in populations. The ecological literature contains thousands of such demonstrations. What can we conclude from this? One of the major conclusions that we can reach is that the potential for evolution by natural selection, which requires genetic variation in populations, is great. However, in order to better understand how such evolutionary change may come about, we need to first understand some aspects of the genetics of populations, or **population genetics.** The theoretical foundations of population genetics were established early in the twentieth century by two investigators named Hardy and Weinberg.

CONCEPT DISCUSSION

Hardy-Weinberg

The Hardy-Weinberg equilibrium model helps identify evolutionary forces that can change gene frequencies in populations.

We defined evolution as a change in a population over time. Since evolution ultimately involves changes in the frequency of heritable traits in a population, we can define evolution more precisely as a change in gene frequencies in a population.



Figure 8.12 Two color forms of *Harmonia axyridis*, the Asian lady beetle. The genetic basis of the color forms of *H. axyridis* is well studied, making it a useful species for studies of population genetics and natural selection.

Therefore a thorough understanding of evolution must include some knowledge of population genetics. Though Mendel is not generally credited with studying the genetics of populations, he included a population level analysis in his paper on inheritance in garden peas (Mendel 1866). In a section of this paper titled, "The Subsequent Generations from the Hybrids," Mendel demonstrated mathematically that if self-fertilization was the only form of fertilization in a population consisting of three genotypes, AA (homozygous dominant), Aa (heterozygous), and aa (homozygous recessive) present in a ratio of one AA individual : two Aa individuals : one aa individual, the frequency of homozygous recessive (aa), and homozygous dominant (AA) individuals would increase in the population. Mendel did not consider what would happen to gene frequencies in his theoretical population if breeding occurred through something other than self-fertilization. Still, his analysis anticipated the field of population genetics, the foundations of which would be laid 42 years later.

Calculating Gene Frequencies

Consider a population of Asian lady beetles of the species Harmonia axyridis (fig. 8.12). Harmonia populations generally include a great deal of variation in color pattern on the wing covers, or elytra, and over 200 color variants are known. Many color forms are so distinctive that early taxonomists described them as different species or even different genera. Genetists in the first half of the twentieth century, especially Chia-Chen Tan and Ju-Chi Li (1934, 1946) and Theodosius Dobzhansky (1937), determined that the variation in color patterns shown by Harmonia is due to the effects of more than a dozen alternative alleles for color pattern. The phenotypic expressions of two of those alleles are shown in figure 8.13. The homozygous "19-signata" genotype of Harmonia, which we can represent as SS, has yellow elytra with several black spots, while the homozygous "aulica" genotype, represented here as AA, has elytra with prominent black borders and a large



Figure 8.13 Color patterns in the Asian lady beetle, *Harmonia axyridis* (after Dobzhansky 1937 and Tan 1946).

oval area of yellow or orange. Tan and Li, who did extensive breeding experiments using *Harmonia* that they collected in southwestern China, found that crosses between 19-signata and aulica genotypes produce heterozygous offspring, indicated here as *SA*, with a color pattern that includes elements of both the 19-signata and the aulica parental forms (fig. 8.13). One of the convenient features of knowing so much about color pattern inheritance in *Harmonia* is that color pattern can be used to determine the genotypes of many individuals.

Now suppose that you sampled the genotypes of *Harmonia* in a tract of forest in Asia and found that the frequency of beetles with genotype *SS* is 0.81 (81%), the frequency of the *SA* genotype is 0.18 (18%), and the frequency of the *AA* genotype is 0.01 (1%). What is the frequency of the *S* and *A* alleles in this population? The frequency in the *S* allele is:

Frequency of SS + 1/2(Frequency of SA) = 0.81 + 1/2(0.18) = 0.81 + 0.09 = 0.90

The frequency of the *A* allele is:

Frequency of AA + 1/2(Frequency of SA) = 0.01 + 1/2(0.18) = 0.01 + 0.09 = 0.10

These calculations show that the frequency of the S allele in this lady beetle population is 0.90, while the frequency of the A allele is 0.10.

Evolutionary ecologists are interested in knowing what factors may change allele frequencies in a population such as that of our hypothetical population of *Harmonia*. Those factors, which we can consider as evolutionary forces, are revealed indirectly by the **Hardy-Weinberg principle**. The Hardy-Weinberg principle states that in a population mating at random in the absence of evolutionary forces, allele frequencies will remain constant.

George H. Hardy, a British mathematician, and Wilhelm Weinberg, a German physician, established their principle, one of the most fundamental of population genetics, in 1908. They did so to address a growing controversy surrounding the applicability of Mendelian genetics to human populations. Hardy was addressing the assertion by a contemporary biologist that a genetically dominant gene introduced to a randomly breeding population would increase in frequency until it reached a frequency of 0.5, producing a ratio of genotypes of one homozygous dominant individual: two heterozygous individuals: one homozygous recessive individual. Because some genetically dominant human traits, such as brachydactyly which produces short fingers, remain rare and do not occur in such simple "Mendelian" ratios, some biologists of the early 1900s claimed that Mendelian genetics does not apply to human populations. Hardy and Weinberg independently revealed the flaws in this line of reasoning and established the Hardy-Weinberg principle.

Let us review how random mating will influence gene frequencies in the *Harmonia* beetle population we just reviewed. Assuming equal fertility of the *SS*, *SA*, and *AA* genotypes, the proportion of *S* and *A* alleles in the population, 0.9 and 0.1, are also the proportions of eggs and sperm carrying the two alleles. With random mating, the probability that any two alleles will be paired in a zygote is determined by the frequency of the alleles in our hypothetical population as follows:

> Proportion of matings that will pair an *S* sperm with an $S \text{ egg} = 0.9 \times 0.9 = 0.81$,

> Proportion of matings that will pair an *S* sperm with an $A \text{ egg} = 0.9 \times 0.1 = 0.09$,

> Proportion of matings that will pair an *A* sperm with an $S \text{ egg} = 0.1 \times 0.9 = 0.09$

and

Proportion of matings that will pair an *A* sperm with an $A \text{ egg} = 0.1 \times 0.1 = 0.01$

The proportion of the three genotypes produced by this random mating will be: SS = 0.81, SA = 0.09 + 0.09 = 0.18, and AA = 0.01. Notice that the proportions of these genotypes in the parents and offspring in the population are the same. If you calculate the allele frequencies from the genotype frequencies in the offspring you will find that they remain at S = 0.90 and A = 0.10, which is what the Hardy-Weinberg principle predicts when mating in a population is random.

We can represent these relationships in a more general way using some basic algebra, if we let p equal the frequency of one allele and q the frequency of the second allele. In the case of the *Harmonia* example just discussed, let p = the frequency of the S allele and q = the frequency of the A allele. Expressing these frequencies in numbers, p = 0.90 and q = 0.10. For a population in Hardy-Weinberg equilibrium in a situation where there are only two alleles at a particular locus, p + q = 1.0. Again referring to the *Harmonia* example, p + q = 0.90 + 0.10 = 1.0. Using this relationship we can calculate the frequency of genotypes in a population in Hardy-Weinberg equilibrium as:

$$(p+q)^2 = (p+q) \times (p+q) = p^2 + 2pq + q^2 = 1.0$$

The result of this calculation is:

$$(0.90)^{2} + 2(0.90 \times 0.10) + (0.10)^{2} = 0.81 + 0.18 + 0.01 = 1.0$$

According to this equation, the frequencies of the genotypes in our hypothetical *Harmonia* population are:

 $p^2 = (0.90)^2 = 0.81 =$ frequency of the SS genotype,

 $2pq = 2(0.90 \times 0.10) = 0.18 =$ frequency of the SA genotype,

and

$$q^2 = (0.10)^2 = 0.01 =$$
 frequency of the AA genotype.

These calculations are equivalent to the combining of alleles that would occur if individuals in the *Harmonia* population mated at random. The mathematics of the Hardy-Weinberg model are further dissected in figure 8.14.

In the equations we just explored, random mating is sufficient to maintain constant genotype and allele frequencies. However, Hardy pointed out in his 1908 paper that in natural populations, other conditions are also required to maintain constant allele frequencies. For instance, Hardy recognized that nonrandom mating or differences in fertility among genotypes can change allele frequencies in a population. The conditions necessary to maintain constant allele frequencies in a population, what is called Hardy-Weinberg equilibrium, are as follows:

- 1. *Random mating*. Nonrandom or preferential mating, in which the probability of pairing alleles is either greater or lower than would be expected based on their frequency in the population, can change the frequency of genotypes.
- 2. *No mutations*. Mutations which add new alleles to the population or change an allele from one form to another have the potential to change allele frequencies in a population and therefore disrupt Hardy-Weinberg equilibrium.
- 3. *Large population size*. Small population size increases the probability that allele frequencies will change from one generation to the next due to chance alone. Change in allele frequencies due to chance or random events is called **genetic drift**. Genetic drift reduces genetic variation in populations over time by increasing the frequency of some alleles and reducing the frequency of some alleles or eliminating others.



Figure 8.14 Anatomy of a Hardy-Weinberg equilibrium equation.

- 4. *No immigration.* Immigration can introduce new alleles into a population or, because allele frequencies are different among immigrants, alter the frequency of existing alleles. In either case immigration will disrupt Hardy-Weinberg equilibrium.
- 5. All genotypes have equal fitness, where fitness is the probability of surviving and reproducing. If different genotypes survive and reproduce at different rates, then gene and genotype frequencies will change in populations.

Hardy-Weinberg equilibrium requires that all five of these conditions be met. How likely is it that all the conditions required for Hardy-Weinberg equilibrium will be present in a natural population? In places and at times the conditions appear to be present. However, it is very likely that one or more of these conditions will not be met and allele frequencies will change. While at first thought it may not appear that the Hardy-Weinberg principle is an important contribution to biology, it is in fact very important. By carefully defining the highly restrictive conditions under which evolution is not expected, the analysis by Hardy and Weinberg leads us to conclude that the potential for evolutionary change in natural populations is often very great.

When a population is not in Hardy-Weinberg equilibrium, the principle helps us to identify the evolutionary forces that may be in play. Observations of natural populations of *Harmonia* indicate that they are often not in Hardy-Weinberg equilibrium. For instance, Dobzhansky (1937) did extensive surveys of *Harmonia* across Asia and found the aulica form in many sites along with the 19-signata form (see fig. 8.13). However, he did not report the intermediate form, 19-signata crossed with aulica (see fig. 8.13). The absence of this intermediate phenotype from Dobzhansky's surveys suggests that the populations he studied were not in Hardy-Weinberg equilibrium.

Why would these intermediate types not be present in sufficient numbers for Dobzhansky to report them? One possible reason is nonrandom mating within the populations. Is there evidence of nonrandom mating by Harmonia? Substantial work on associations of color variants of Harmonia has been done in Japan. Taku Komai and Yasushi Hosino (1951) found that Harmonia with different color patterns had different habitat associations in a village landscape near Nagoya, Japan. Differences in habitat preferences among variants within a population can contribute to nonrandom mating. In addition, other Japanese researchers have more recently made direct observations of nonrandom mating in Harmonia. Naoya Osawa and Takayoshi Nishida (1992) observed preferential mating based on color pattern in a population of Harmonia near Kyoto, Japan. In 1998, H. Ueno, Y. Sato, and K. Tsuchida observed preferential mating in another Harmonia population in Japan based on size not on color pattern.

Meanwhile, other researchers have documented changes in gene frequencies in *Harmonia* populations near Vladisvostok, Russia, that have taken place since the 1920s, when they were studied by Dobzhansky. L. Bogdanov and N. Gagal'chii (1986) collected *Harmonia* near Vladisvostok and compared the frequencies of color variants within their collections to those found by Dobzhansky (1937) approximately one-half century earlier. What they found was a great departure from Hardy-Weinberg equilibrium. While most color variants decreased in frequency, 19-signata increased by 30%. Meanwhile, the aulica color variant had disappeared entirely. The work by Bogdanov and Gagal'chii clearly documents changes in genotype frequencies within these populations. In other words, though they did not document the mechanisms involved, they found evidence for evolutionary change.

In the remaining sections of chapter 8 we will discuss examples in which one or more of the conditions for Hardy-Weinberg equilibrium have not been met and where evolutionary change has occurred in populations as a consequence. We begin this discussion with a general overview of the process of natural selection.



Figure 8.15 Three principle forms of natural selection: (a) stabilizing selection, (b) directional selection, and (c) disruptive selection.



As we saw in the introduction to chapter 8, Darwin was one of the first people to recognize the biological significance of varia-

tion among individuals in a population. The biological significance of the variation that Darwin recognized stemmed from an inference that he drew. His inference was that some phenotypes in a population would have an advantage over others under particular environmental circumstances. That is, the phenotypic characteristics of some individuals, for instance, larger or smaller size, different body proportions, lighter or darker pigmentation, or higher or lower metabolic rate, would result in higher rates of reproduction and survival compared to other individuals with other phenotypic characteristics. In other words, some individuals in a population, because of their phenotypic characteristics, produce more offspring that themselves live to reproduce.

While the basic concept of natural selection is easy enough to grasp, natural selection does not a take the same form everywhere and at all times. Rather, natural selection can act against different segments of the population under different circumstances and can produce quite different results. Natural selection can lead to change in populations but it can also serve as a conservative force, impeding change in a population. Natural selection can increase diversity within a population or decrease diversity. Let's begin our discussion of natural selection with a process that conserves population characteristics.

Stabilizing Selection

One of the conclusions that we might draw from the discussion of the Hardy-Weinberg equilibrium model is that most populations have a high potential for evolutionary change. However, our observations of the natural world suggest that species can remain little changed for generation after generation. If the potential for evolutionary change is high in populations, why does it not always lead to obvious evolutionary change at least on the short term? There

are many reasons for apparent absence of change in populations. For example, one form of natural selection, called **stabilizing selection**, can act to impede changes in populations.

Stabilizing selection acts against extreme phenotypes and as a consequence favors the average phenotype. Figure 8.15*a* pictures stabilizing selection, using a normal distribution of body size. Under the influence of stabilizing selection, individuals of average size have higher survival and reproductive rates, while the largest and smallest individuals in the population have lower rates of survival and reproduction. As a consequence of stabilizing selection, a population tends to sustain the

same phenotype over time. Stabilizing selection occurs where average individuals in a population are best adapted to a given set of environmental conditions. If a population is well adapted to a given set of environmental circumstances, stabilizing selection may sustain the match between prevailing environmental conditions and the average phenotype within a population. However, stabilizing selection for a particular trait can be challenged by environmental change. In the face of environmental change the dominant form of selection may be directional.

Directional Selection

If we examine the fossil record or trace the history of wellstudied populations over time, we can find many examples of how populations have changed in many characteristics over time. For instance, there have been remarkable changes in body size or body proportions in many evolutionary lineages. Such changes may be the result of **directional selection**.

Directional selection favors an extreme phenotype over other phenotypes in the population. Figure 8.15b presents an example of directional selection, again, using a normal distribution of body size. In this hypothetical situation, larger individuals in the population realize higher rates of survival and reproduction, while average and small individuals have lower rates of survival and reproduction. As a consequence of these differences in survival and reproduction, the average phenotype under directional selection changes over time. In the example shown in figure 8.15b, average body size increases with time. Directional selection occurs where one extreme phenotype has an advantage over all other phenotypes. However, there are circumstances in which more than one extreme phenotype may have an advantage over the average phenotype. Such a circumstance can lead to diversification within a population.

Disruptive Selection

There are populations that do not show a normal distribution of characteristics such as body size. In a normal distribution such as those depicted in figures 8.15*a* and 8.15*b*, there is a single peak, which coincides with the population mean. That is, the average phenotype in the population is the most common and all other phenotypes are less common. However, in some populations there may be two or more common phenotypes. In many animal species, for example, males may be of two or more discrete sizes. For example, it appears that in some animal populations small and large males have higher reproductive success than males of intermediate body size. In such populations, natural selection seems to have produced a diversity of male sizes. One way to produce such diversity is through **disruptive selection**.

Disruptive selection favors two or more extreme phenotypes over the average phenotype in a population. In figure 8.15*c*, individuals of average body size have lower rates of survival and reproduction than individuals of either larger or smaller body. As a consequence, both smaller and larger individuals increase in frequency in the population over time. The result is a distribution of body sizes among males in the population with two peaks. That is, the population has many large males and many small males but few of intermediate body size.

Figure 8.15*b* and 8.15*c* indicate change in the frequencies of phenotypes in the two hypothetical populations after a period of natural selection. This change depends on the extent to which genes determine the phenotype upon which natural selection acts. This dependence is the focus of the following concept discussion.



Evolution by Natural Selection

The extent to which phenotypic variation is due to genetic variation determines the potential for evolution by natural selection.

The most general postulate of the theory of natural selection is that the environment determines the evolution of the anatomy, physiology, and behavior of organisms. This is what Darwin surmised as he studied variation among populations and species in different environments. Coincidentally, one of the clearest demonstrations of natural selection has resulted from studies of populations of Galápagos finches, which are reviewed in chapter 11 (pp. 000–000) and chapter 13 (pp. 000–000). Those studies showed that the quantity and quality of available food exerts strong selection on beak size in finch populations. Here we review additional studies that also provide evidence for Darwin's bold hypothesis that natural selection by the environment can result in evolutionary change in populations.

Evolution by Natural Selection and Genetic Variation

Darwin was keenly aware that the only way natural selection can produce evolutionary change in a population is if the phenotypic traits upon which natural selection acts can be passed from generation to generation. In other words, evolution by natural selection depends upon the heritability of traits. We can define **heritability** of a trait—usually symbolized as h^2 in a broad sense as the proportion of total phenotypic variation in a trait, such as body size or pigmentation, that is attributable to genetic variance. In equation form, heritability can be expressed as:

 $h^2 = V_G / V_P$

Here V_G represents genetic variance and V_P represents phenotypic variance. (We reviewed how to calculate variance in chapter 6, p. 162.) Many different factors contribute to the amount of phenotypic variance in a population. We will subdivide phenotypic variance into only two components: variance in phenotype due to genetic effects, V_G , and variance in phenotype due to environmental effects on the phenotype, V_E . Subdividing V_P in the heritability equation given above produces the following:

$$h^2 = V_G / V_G + V_E$$

This highly simplified expression for heritability has important implications so let's take a little space to examine it. First, let's consider environmental variance, V_E . Environment has substantial effects on many aspects of the phenotype of organisms. For instance, the quality of food eaten by an animal can contribute significantly to the growth rate of the animal and to its eventual size. Similarly, the amount of light, nutrients, temperature, and so forth, affect the growth form and size of plants. So, when we consider a population of plants or animals, some of the phenotype that we might measure will be the result of environmental effects, that is, V_E . However, we are just as familiar with the influence of genes on phenotype. For example, some of the variation in stature that we see in a population of animals or plants will generally result from genetic variation among individuals in the population, that is, V_G .

What our equation says is that the heritability of a particular trait depends on the relative sizes of genetic versus environmental variance. Heritability increases with increased V_G and decreases with increased V_E. Imagine a situation in which all phenotypic variation is the result of genetic differences between individuals and none results from environmental effects. In such a situation, V_E is zero and $h^2 = V_G/V_G + V_E$ is equal to $h^2 = V_G/V_G$ (since $V_E = 0$), which equals 1.0. In this case since all phenotypic variation is due to genetic effects, the trait is perfectly heritable. We can also imagine the opposite circumstance in which none of the phenotypic variation that we observe is due to genetic effects. In this case, V_G is zero and so the expression $h^2 = V_G/V_G + V_E$ also equals zero. Because all of the phenotypic variation we observe in this population is due to environmental effects, natural selection cannot produce evolutionary change in the population. Generally, heritability of traits falls somewhere in between these extremes in the very broad region where both environment and genes contribute to the phenotypic variance shown by a population. For instance, Peter Boag and Peter Grant (1978) estimated bill width in the Galápagos finch Geospiza fortis to have a heritability of 0.95. By comparison they estimated that bill length in the species has a heritability of 0.62. In a study of morphological variation in the water lily leaf beetle, a team of Dutch scientists (Pappers et al. 2002) found that body length and mandible width had heritabilities of between 0.53 and 0.83. Now that we have established the requirement of heritable variation in a trait for evolution in that trait, let's review studies that have explored evolution by natural selection in nature.



Figure 8.16 A brown anole, *Anolis sagrei*, jumping. Limb length is known to be highly correlated with the types of perches used by *Anolis* species.

Adaptive Change in Colonizing Lizards

As we reviewed cases of physiological, anatomical, or behavior features of organisms, especially in section II of the text, we assumed that they were the result of adaptation of populations through the process of natural selection. However, we have reviewed few studies that have documented the process of natural selection. Why is it so important to make this distinction? In science we must always guard against mixing pattern and process or evidence and interpretation. In this section we address this omission by reviewing elegant studies that have documented natural selection in progress.

One of those studies was conducted by Jonathan Losos, Kenneth Warheit, and Thomas Schoener on lizards of the genus Anolis (Losos, Warheit, and Schoener 1997). Approximately 150 species of Anolis inhabit the islands of the Caribbean Sea and another 250 are found in Central and South America (fig. 8.16). This great diversity of lizards in a single genus includes a great amount of variation in size and body proportions. The anatomy of Anolis lizards, especially the length of their hind limbs, appears to reflect selection for effective use of vegetation. The attribute of vegetation that appears to be most significant in selection for hind limb length is the diameter of surfaces available for perching. Hind limb length in Anolis populations appears to be the result of a trade-off between selection for maximum speed (lizards with longer hind limbs run faster) and selection for moving efficiently on narrow branch surfaces (lizards with shorter hind limbs move more efficiently on narrow surfaces).

Losos, Warheit, and Schoener used replicated field experiments to study natural selection for changes in morphology in *Anolis* lizard populations. They designed their experiments in such a way that they could make very specific predictions concerning expected morphological changes among lizard populations. Losos and his colleagues captured adult *Anolis*

sagrei on Staniel Cay in the Bahama Islands and then introduced them in groups of 5 to 10 lizards, at a ratio of 2 males:3 females, to 11 small islands in 1977 and to three more in 1981. None of these small islands had their own lizard populations, probably because hurricanes periodically eliminate lizards from them. The islands also differed greatly in their vegetative cover, which ranged in maximum height from 1 to 3 m on the different islands, but all had substantially lower vegetation than Staniel Cay, which supports some trees over 10 m tall.

Let us reflect on the conditions of the experiment. All the introduced lizards were drawn from the same source population on Staniel Cay, which could serve as a reference population. The islands onto which the lizards were introduced each supported somewhat different vegetation. Therefore, if vegetation is a primary agent selecting for differences in hind limb size, the morphology of the introduced populations should change from that of the source populations, but they should also differ from each other, depending on the vegetation on each small island. Losos, Warheit, and Schoener made two specific predictions: (1) the extent to which the colonizing populations change morphologically from the source population will correlate with the amount of difference in vegetative structure on the experimental islands and Staniel Cay, and (2) the Anolis populations on the experimental islands and Staniel Cay should show a significant correlation between relative hind limb length within populations and average perch diameter used on the islands.

After the lizards had occupied the experimental islands for 10 to 14 years, Losos and his colleagues returned to the islands and measured lizard morphology and their distributions on the local vegetation. Both predictions of the researchers were well supported by the results of their study. First, they found a positive correlation between the difference in vegetative height on experimental islands compared to Staniel Cay and the degree to which introduced lizards diverged from the ancestral population (fig. 8.17). Second, the hind limb length in the lizard populations was positively correlated with the average perch diameter the lizards used on each island (fig. 8.18). That is, on islands where lizards use perches of larger diameter, they have longer hind limbs.

The researchers point out that their results indicate that colonizing populations can adapt rapidly to new environmental conditions. However, they also caution that while their results are consistent with the effects of natural selection for changed morphology, they do not demonstrate unequivocally that the colonizing populations have evolved. What would we have to know to demonstrate an evolutionary response? We would have to know that the composition of the founding populations had changed genetically and that some of those genetic changes were responsible for the changes in morphology observed by Losos and his research partners. If the founding populations have not changed genetically, what is another possible source of their changed morphology? The environ-



Figure 8.17 Relationship between the difference in height of vegetation between the home island, Staniel Cay, and island of introduction and change in lizard morphology after their introduction (data from Losos et al. 1997).



Figure 8.18 Relationship between hind limb length in *Anolis sagrei* and perch diameters on experiment islands (data from Losos et al. 1997).

mental differences on the different islands, especially perch diameter, may have induced different developmental patterns that resulted in different hind limb lengths in the different lizard populations. At this point we cannot rule out the possibility that lizards on experimental islands underwent a developmental change and not an evolutionary change. To eliminate this possibility requires genetic studies. In the next study on rapid adaptation by soapberry bugs, the researchers collected extensive genetic information to document the operation of natural selection. Information Questions Hypothesis Predictions Testing

Investigating the Evidence

Estimating Heritability Using Regression Analysis

As we have seen, the extent to which phenotypic variation in a trait is determined by genetic variation affects its potential for that trait to evolve by natural selection. In other words, the potential for a trait to evolve is affected by the trait's heritability. How can we estimate the heritability of a particular trait? One common method is through regression analysis. Regression analysis is a statistical technique used to explore the extent to which one factor, called the independent variable (usually symbolized as X) determines the value of another variable, which we call the dependent variable (usually represented by the symbol Y). In regression analysis, we construct X-Y plots as we did when we explored scatter plots and correlation (Investigating the Evidence, Chapter 7, p. 186). However, regression analysis is used to determine the equation for a line, called a regression line, that best fits the relationship between X and Y. When the relationship between X and Y follows a straight line, the regression equation takes the following form:

Y = bX + a

In this equation, *a* is the point at which the line crosses the Y axis, which is called the Y intercept, and *b*, which is the slope of the line, is the **regression coefficient**.

Let's use a natural system to learn more about regression analysis and its use in heritability studies. In heritability studies, we are interested in the extent to which the characteristics of parents determine the characteristics of offspring. For instance, the team of Dutch scientists studying water lily leaf beetles (Pappers et al. 2002) explored the heritability of body length in different populations of the beetle. To determine the heritability of body length, they conducted regression analyses using the body length of parents as the independent variable, and body length of the offspring as the dependent variable. Because each of the parents contributes to the genotype of the offspring, the value used for parental body length is the "mid-parent body length," which is the average of the two parents' body lengths. Let's consider the relationships between length of parents and offspring, and use regression analysis to estimate heritability of body length in some hypothetical populations of water lily leaf beetles.

Consider the three scatter plots shown in figure 1 and the lines drawn through the scatter of points. Again, these are much like the scatter plots we examined in chapter 7 but with regression lines drawn through each. The regression coefficient in each of the graphs indicates the level of heritability in the three hypothetical populations. In population a, the regression coefficient of 0.00 indicates that there is no relationship between parental body length and the body length of offspring. This result is apparent from just the scatter plot, which shows that parents of any length, large or small, can have small or large offspring. In this population it appears that the variation in body length among the offspring is determined entirely by environmental effects. In contrast, body length has a heritability of 0.52 in population b and 1.00 in population c. What do these values indicate? With a heritability of 0.52, we can conclude that about half of the variation in body length in population b results from genetic effects, and about half from environmental effects, such as food quality, temperature, and so forth. The regression coefficient of 1.00 in population c indicates that all the variation in body length in the offspring in that population is the result of genetic effects.

What are the evolutionary implications of the patterns shown in figure 1? The main evolutionary consequence is that natural selection on body size could lead to evolutionary change in body size in populations b and c but not in population a.



Figure 1 Regression analyses indicating degree of heritability of body length in three hypothetical populations of water lily leaf beetles.

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Section III Population Ecology

Rapid Adaptation by Soapberry Bugs to New Host Plants

As discussed in chapter 6, herbivores must overcome a wide variety of physical and chemical defenses evolved by plants. As a consequence, plants theoretically exert strong selection on herbivore physiology, behavior, and anatomy. While herbivore adaptation to plant defenses are generally inferred from the juxtaposition of plant defenses and herbivore characteristics, few studies have documented the process of herbivore adaptation. A notable exception is provided by studies of the soapberry bug and its evolution on new host plants.

The soapberry bug, *Jadera haematoloma*, feeds on seeds produced by plants of the family Sapindaceae. Soapberry bugs use their slender beaks to pierce the walls of the fruits of their host plants. To allow the bug to feed on the seeds within the fruit, the beak must be long enough to reach from the exterior of the fruit to the seeds. The distance from the outside of the fruit wall to the seeds varies widely among potential host species. Thus beak length should be under strong selection for appropriate length.

Scott Carroll and Christin Boyd (1992) reviewed the history and biogeography of the colonization of new host plants by soapberry bugs. Historically, soapberry bugs fed on three main host plants in the family Sapindaceae: the soapberry tree, Sapindus saponaria v. drummondii, in the southcentral region of the United States, the serjania vine, Serjania brachycarpa, in southern Texas, and the balloon vine, Cardiospermum corindum, in southern Florida. During the second half of the twentieth century three additional species of the plant family Sapindaceae were introduced to the southern United States. The round-podded golden rain tree, Koelreuteria paniculata, from east Asia and the flatpodded golden rain tree, K. elegans, from southeast Asia are both planted as ornamentals, while the subtropical heartseed vine, Cardiospermum halicacabum, has invaded Louisiana and Mississippi. At some point after their introduction, some soapberry bugs shifted from their native host plants and began feeding on these introduced plant species.

Carroll and Boyd painstakingly reconstructed the history of the colonization of the southern United States by new species of host plants and colonization of these new plants by soapberry bugs. Fortunately, extensive historical museum collections of plants and insects allowed them to assemble the history of a fascinating host shift by an herbivorous insect. They were particularly interested in determining whether the beak length had changed in soapberry bugs that shifted from native to introduced host plants.

Figure 8.19 contrasts the fruit radius of native and introduced host plants in Florida and the south central United States. In Florida the fruit of the native host plant *C. corindum* has a much larger radius than the fruit of the introduced *K. elegans* (11.92 mm versus 2.82 mm). In the south central United States soapberry bugs shifting to introduced host



Figure 8.19 Comparison of the radius of fruits produced by native and introduced species of Sapindaceae (data from Carroll and Boyd 1992).

plants faced the opposite situation. There, the fruit of the native *S. saponaria* has a smaller radius (6.05 mm) than the fruits of the introduced *K. paniculata* (7.09 mm) and *C. halicacabum* (8.54 mm).

Carroll and Boyd reasoned that if beak length was under natural selection to match the radius of host plant fruits, bugs shifting to the introduced plants in Florida should be selected for reduced beak length, while those shifting to introduced hosts in the south central United States should be selected for longer beaks. Figure 8.20 shows the relationship between soapberry beak length and the radius of fruits of their host plants. As you can see, there is a close correlation between fruit radius and beak length.

At this point we should ask whether the differences in beak length observed by Carroll and Boyd might be developmental responses to the different host plants. In other words, are the differences in beak length due to genetic differences among populations of soapberry bugs or were they induced



Figure 8.20 Relationship between fruit radius and beak length in populations of native and introduced species of soapberry bugs (data from Carroll and Boyd 1992).

by the different host plants? Fortunately, Carroll reared juvenile bugs from the various populations on alternative host plants so we can answer this question. As it turns out, the differences in beak length observed in the field among bugs feeding on the various native and introduced host plants were retained in bugs that developed on alternative hosts. Thus, we have more information than is available for the *Anolis* lizard study reviewed earlier. Here we have evidence for a genetic basis for interpopulational differences among soapberry bugs. Consequently, we can conclude that the differences in beak length documented by Carroll and Boyd were likely the result of natural selection for increased or decreased beak length.

Scott Carroll, Stephen Klassen, and Hugh Dingle (1997, 1998) have done extensive additional studies of soapberry bugs that document substantial genetic differences between populations living on native versus introduced plants in the family Sapindaceae. Significantly, from the perspective of natural selection, the differences between these populations of soapberry bugs are great enough that both show reduced reproduction and survival when forced to live on the alternative host plants. That is, when soapberry bugs that normally live on native host plants are moved to introduced plants, their survival and reproductive rates decrease. However, when soapberry bugs that now live on introduced plants are moved to native plants, which their ancestors fed on only 30 to 100 years ago, their reproductive and survival rates also decrease. These additional studies of the genetic differences between soapberry bug populations provide additional evidence that populations of these bugs living on different host plants have undergone natural selection for traits that favor their survival and reproduction on their plant hosts.

CONCEPT DISCUSSION

Change Due to Chance

Random processes, such as genetic drift, can change gene frequencies in populations, especially in small populations.

While we may often think of evolutionary change as a consequence of predictable forces such as natural selection which favors, or disfavors, particular genotypes over others, allele frequencies can change as a consequence of random processes such as genetic drift. Genetic drift is theoretically most effective at changing gene frequencies in small populations such as those that inhabit islands. In the following examples, we consider the effects of genetic drift on populations on isolated mountaintops and on islands.

Evidence of Genetic Drift in Chihuahua Spruce

One of the greatest concerns associated with fragmentation of natural ecosystems due to human land use is that reducing habitat availability will decrease the size of animal and plant populations to the point where genetic drift will reduce the genetic diversity within natural populations. Are these concerns wellfounded? The Hardy-Weinberg principle predicts that reducing small population sizes will lead to reduced genetic variation. However, we do not have to rely solely on theory to learn of the effects of habitat fragmentation on genetic diversity.

Many natural populations have undergone fragmentation as a consequence of changing climates and natural habitat fragmentation. One of those is the Chihuahua spruce, Picea chihuahuana, which is now restricted to the peaks of the Sierra Madre Occidental in northern Mexico. During the Pleistocene glacial period when the global climate was much cooler, spruce were found much farther south in Mexico and in more extensive populations. However, following the end of the Pleistocene and the onset of the warmer recent, or Holocene period, spruce populations moved northward and to higher elevations. Today, all spruce populations in Mexico are restricted to small, highly fragmented areas of subalpine environment in the mountains of states of Chihuahua and Durango. On these high mountains, Chihuahua spruce lives in an 800 km long band along the crest of the Sierra Madre Occidental at elevations between 2,200 and 2,700 m. On a local scale, the species is mainly found on cooler north-facing slopes along well-watered stream corridors, which are the microclimates where you would expect to find the descendants of an ice age relictual population. In these mountain refuges, Chihuahua spruce persists as far south as 23°30' N latitude, just south of the Tropic of Cancer.

While the spruce of Durango have not been censused yet, all the Chihuahua spruce in the State of Chihuahua have been located and counted. Local populations of the species range in size from 15 to 2,441 individuals. This situation presents itself as a natural experiment on the effects of population size and habitat fragmentation on genetic diversity in populations. The opportunity for such studies was pursued by a joint team of U.S. and Mexican scientists (Ledig et al. 1997). F. Thomas Ledig and Paul D. Hodgskiss from the USDA Forest Service and Virginia Jacob-Cervantes and Teobaldo Eguiluz-Piedra of the Universidad Autonoma of Chapingo, Mexico, combined efforts to determine whether Chihuahua spruce has lost genetic diversity as a consequence of reduced population size following climatic warming after the end of the last ice age. They were also interested in whether reduced genetic diversity may be contributing to continuing decline of the species and its potential for extinction.

Ledig and his colleagues were particularly interested in the relationship between genetic diversity and population size. They used a technique called starch gel electrophoresis to determine the number of alleles present for 16 enzyme systems. Enzymes are of course gene products, and greater numbers of the various forms of an enzyme, which are called **allozymes**, indicate higher levels of genetic diversity in a population. The team assayed allozyme diversity for 24 genes, or **loci**, in seven populations ranging in size from 17 to 2,441 individuals.

As you might predict from the Hardy-Weinberg principle, Ledig and his colleagues found a significant positive correlation between population size and genetic diversity of their study populations. Figure 8.21 indicates that the smallest populations of Chihuahua spruce have much lower levels of genetic diversity than the largest populations. These results are consistent with the Hardy-Weinberg principle, which predicts that genetic drift will be most important in small populations.

How might drift occur in populations of spruce living on isolated mountain peaks in western Mexico and how might genetic drift reduce genetic variation in spruce populations? Imagine a population of 15 Chihuahua spruce on a mountain peak in the Sierra Madre Occidental at the beginning of July when the summer rains begin. The forest is dry after a long spring drought and as the lightning produced by a thunderstorm begins to strike the mountain, one bolt hits one of the spruce trees. The tree explodes as its interior water is turned into superheated steam, sending showers of splintered wood 50 m in all directions. The spruce tree then catches fire and the flames engulf two neighboring spruce trees before the ensuing torrential rains put out the fire. The result is a small spot fire that has killed three trees. The deaths of three trees would make very little difference in a population of several thousand. However, in a population of just 15, three trees represent 20% of the individuals. When individuals are removed from very small populations their removal often reduces the frequency of some alleles; such events will eventually eliminate some alleles entirely from a small population.



Figure 8.21 Relationship between population size and genetic diversity of chihuahua spruce, *Picea chihuahuana*, populations (data from Ledig et al. 1997).

It seems likely that genetic drift is changing allele frequencies and reducing overall genetic diversity in populations of Chihuahua spruce. However, this is one species occupying relictual environments in one corner of North America. Would we see consistent reductions in genetic diversity if we examined a larger number of populations inhabiting insular or fragmented environments? The next study addresses this question for both plants and animals.

Genetic Variation in Island Populations

Richard Frankham (1997) of the Centre for Biodiversity and Bioresources at Macquarie University in Sydney, Australia, compared the genetic diversity of island and mainland populations of both animals and plants. His study was motivated by the fact that rates of extinction in historic times have been much higher for island populations compared to mainland populations. Frankham developed the idea that because lower genetic variation within a population indicates lower potential for evolutionary responses to environmental challenge, lower genetic variation within island populations may be partly responsible for their greater vulnerability to extinction compared to mainland populations. However, when he reviewed what was known about the relative genetic variation in island and mainland populations, he encountered a great deal of uncertainty. Frankham undertook his study to fill this information gap. He posed two main questions. Do island populations of sexually reproducing species have lower genetic variation than comparable mainland populations? Do endemic island populations, which have lived in isolation on islands long enough to diverge substantially from mainland populations, have lower genetic variation than nonendemic mainland populations?



Figure 8.22 Comparison of genetic variation in mainland versus island populations (data from Frankham 1997).



Figure 8.23 Comparison of genetic variation in mainland versus island populations (data from Frankham 1997).

Frankham addressed these questions by thoroughly searching the extensive literature on genetic variation in animal and plant populations. His research uncovered 202 comparisons of genetic diversity in island versus mainland populations and 38 comparisons of genetic diversity in endemic species on islands versus related mainland species populations. The organisms in the analysis ranged from moose and wolves to toads, insects, and trees. The results of Frankham's analyses clearly support the hypothesis that genetic diversity is lower in island populations (fig. 8.22). Out of 202 mainlandisland comparisons, 165 showed higher genetic variation in mainland populations compared to 37 which indicated higher genetic variation in island populations. Frankham found that the trend toward higher genetic variation in mainland populations was even stronger when he compared island endemic populations versus mainland populations of closely related species (fig. 8.23). Out of 38 endemic island-mainland comparisons, 34 showed higher genetic variation in mainland populations compared to 4 which indicated higher genetic variation in endemic island populations.

Frankham's analysis takes us well beyond the study of how population size is related to genetic variation in populations of Chihuahua spruce (Ledig et al. 1997). It appears that in general, genetic variation is lower in isolated and generally smaller, island populations. What is the ecological significance of this result? One very fundamental point of interest is that genetic variation is the substrate upon which the environment can act to produce evolutionary change by natural selection. Reduced genetic variation indicates a lower potential for a population to evolve. One of Frankham's motivations for his study was to explore the possibility that lower genetic variation in island populations may contribute to the higher rates of extinction of island populations. By demonstrating that island populations have lower genetic variation than mainland populations, he shows that genetic factors cannot be eliminated as a contributor to the higher extinction rates observed on islands. However, while this study keeps genetic diversity alive as a viable hypothesis, it does not in itself demonstrate a connection between extinction rates and genetic diversity. That connection was made in a study published a year after Frankham's results appeared in print.

Genetic Diversity and Butterfly Extinctions

The landscape of Åland in southwestern Finland is a patchwork of lakes, wetlands, cultivated fields, pastures, meadows, and forest (see fig. 21.12). Here and there in this well-watered land-scape you can find dry meadows that support populations of plants, *Plantago lanceolata* and *Veronica spicata*, that act as hosts for the Glanville fritillary butterfly, *Melitaea cinxia* (fig. 8.24). As discussed in chapter 21, the meadows where *Melitaea* lives vary greatly in size, and *Melitaea* population size increases directly with the size of meadows (see fig. 21.13).



Figure 8.24 Long-term studies of the Glanville fritillary butterfly, *Melitaea cinxia*, have provided exceptional insights into the relationship between population size and genetic diversity.

Careful studies of these populations by Ilkka Hanski, Mikko Kuussaari, and Marko Nieminen (1994) showed that small populations of *Melitaea* living in small meadows were most likely to go extinct.

Several factors likely influence the greater vulnerability of small populations to extinction. However, what role might genetic factors, especially reduced genetic variation, play in the vulnerability of small populations to extinction? Richard Frankham and Katherine Ralls (1998) point out that one of the contributors to higher extinction rates in small populations may be **inbreeding.** Inbreeding, which is mating between close relatives, is more likely in small populations. Combining already low genetic variation in small populations with a high rate of inbreeding has several negative impacts on populations, including reduced fecundity, lower juvenile survival, and shortened life span.

Ilik Saccheri and five coauthors (1998) reported one of the first studies giving direct evidence that inbreeding contributes to extinctions in wild populations. Saccheri and his colleagues studied 1,600 dry meadows and found Melitaea in 524, 401, 384, and 320 of the meadows in 1993, 1994, 1995, and 1996, respectively. Over this period they documented an average of 200 extinctions and 114 colonizations of meadows annually. As you can see, these populations are highly dynamic. In order to determine the extent that genetic factors, especially inbreeding, may contribute to extinctions, Saccheri and his colleagues conducted genetic studies on populations of *Melitaea* in 42 of the meadows. They estimated heterozygosity, an indicator of genetic variability, with respect to seven enzyme systems and one locus of nuclear microsatellite DNA. The researchers used the level of heterozygosity within each meadow population as an indicator of inbreeding, with low heterozygosity indicating high levels of inbreeding.

The results of the study indicated that influence of inbreeding on the probability of extinction was very significant. It turned out that the populations with the highest levels of inbreeding (lowest heterozygosity) had the highest probabilities of extinction. Saccheri and his colleagues found a connection between heterozygosity and extinction through effects on larval survival, adult longevity, and egg hatching. Females with low levels of heterozygosity produced smaller larvae fewer of which survived to the winter dormancy period. Pupae of mothers with low heterozygosity also spent more time in the pupal stage, exposing them to greater attack by parasites. In addition adult females with low heterozygosity had lower survival and laid eggs with a 24 to 46% lower rate of hatching. These effects have the potential to reduce the viability of local populations of *Melitaea*, which are made up of individuals of low heterozygosity (low genetic variation), and increase their risk of local extinction.

We have seen how the small population size and isolation can influence the genetic structure of populations of many kinds of organisms, including the Chihuahua spruce isolated in cool moist microenvironments in the mountains of Mexico and the Glanville fritillary, *Melitaea* in the dry meadow environments of southwestern Finland. In situations like these, chance plays a significant role in determining the genetic structure of populations.

APPLICATIONS & TOOLS

Estimating Genetic Variation in Populations

In chapter 8 we have focused considerable attention on genetic variation in populations. Here we return to genetic variation to review some historical and recent methods used to measure this significant aspect of population structure. How did the scientists whose work we discussed in this chapter study genetic variation in populations? The earlier research by Clausen, Keck, and Hiesey (1940) used transplant experiments to detect genetic differences among populations. Later research on genetic variation in Chihuahua spruce (Ledig et al. 1997) and in the Glanville fritillary butterfly (Saccheri et al. 1998) used techniques developed in molecular biology. Though the number of molecular-based studies of genetic variation is growing at a tremendous rate, transplant experiments remain a useful tool for studying genetic differences among populations.

Transplant Experiments

The classical studies of variation among *Potentilla glandulosa* by Clausen, Keck, and Hiesey (1940) provide a model for the design and interpretation of transplant, or common garden, studies. Figure 8.25 shows photos of the transplant gardens used by Clausen and his colleagues at Stanford (lowland elevation 30 m), Mather (mid-elevation 1,400 m), and Timberline (alpine 3,050 m). Because these photos show the local natural vegetation in the background, they give a visual impression of the biomes in which the gardens were established. The natural vegetation at the sites were temperate woodland at the lowland elevation site, temperate coniferous forest at the mid-elevation site, and subalpine forest grading into alpine meadow at the alpine site.

As you would predict from our earlier review of the influence of elevation on climate (see fig. 2.38), the climates at the three study sites differed substantially. The growing seasons were 12 months at the lowland elevation site, 5 1/2 months at the mid-elevation site, and approximately 2 months at the alpine site. Minimum monthly temperatures ranged from -2° C at the lowland elevation site and -10° C at the mid-elevation site down to -22° C at the alpine site. Maximum monthly temperatures ranged from 35° C at the lowland and mid-elevation sites to 25° C at the alpine site. While there was no snow at the lowland site, snow cover at the mid-elevation site generally persisted from October to April. Meanwhile, at the alpine site snows began in September and continued to approximately the first of July. This range of conditions certainly offers the potential for local adaptation and genetic variation among



(a)



(b)



(c)

Figure 8.25 Photos of gardens used by Clausen, Keck, and Hiesey (1940) in transplant experiments with *Potentilla glandulosa*. The photos show (a) the Timberline (3,050 m), (b) Mather (1,400 m), and (c) Stanford (30 m) sites.

local populations of *P. glandulosa*. Clausen and his colleagues designed their transplant experiments to reveal those differences if they existed.

Figure 8.26 summarizes the details of the P. glandulosa transplant experiments. The upper panel of figure 8.26 sketches how plants from each study area were transplanted to the other garden sites where they were grown beside the local plants. How did Clausen, Keck, and Hiesey's transplant experiment indicate genetic differences among local populations of P. glandulosa? To understand how their results showed genetic differences we need to consider how the results would have looked if there were no genetic differences among local populations. This hypothetical situation is presented as a null hypothesis in the middle panel of figure 8.26. If there were no genetic differences among populations, all plants would have shown the same characteristics at each site. Contrast these uniform responses, expected if the null hypothesis were true, with the representation of the actual results in the lower panel. Each population showed unique growth responses at each of the transplant gardens. On the basis of differences in growth, flower number (see fig. 8.4), survival, and several other characteristics, Clausen and his coauthors concluded that the study populations of P. glandulosa differed genetically.

The continued utility of transplant experiments is shown by the results of Tracy's (1999) study of variation among chuckwalla lizard, Sauromalus, populations (see fig. 8.10). In that study Tracy transplanted lizards from different regions into a controlled laboratory environment. Since modern molecular methods allow us to look directly at genetic differences among populations, why would some biologists continue to use transplant experiments? One advantage of transplant experiments is that they are simple and require little investment in technology. What are some of the disadvantages of transplant experiments? They often require more time and labor to carry out and they can be applied to a limited number of organisms. While transplant experiments continue to be useful, modern molecular techniques are allowing evolutionary ecologists to explore details of genetic variation within and among populations that would be impossible without these modern techniques.

Molecular Approaches to Genetic Variation

The tools of molecular biology can be used to determine the genotypes of individuals either by looking at products of genes, such as enzymes, or by analyzing DNA directly. In chapter 8, Ledig and his coauthors (1997) estimated genetic variation in populations of Chihuahua pine by measuring variation in the allozymes of 16 different enzyme systems (see fig. 8.21). Because allozymes of the same enzyme are the products of different alleles of the same gene locus, the number of allozymes produced by a population can be used as an indicator of genetic variation within the population. Many studies of enzymes examine all **isozymes**, which are all enzymes with the same biochemical function. Different isozymes may be produced by the same or



Figure 8.26 A common garden approach to studying genetic variation among populations of *Potentilla glandulosa* (data from Clausen, Keck, and Hiesey 1940).

different loci. Though enzyme studies remain a useful and powerful tool in evolutionary studies, genetic variation is increasingly assessed by looking directly at DNA. For instance, Saccheri and his colleagues (1998) used a combination of enzyme and direct DNA studies to characterize the genetic structure of populations of the Glanville fritillary butterfly. A detailed review of molecular methods used to study genetic variation is well beyond the scope of this discussion. However, reviewing at least the basics of some of the common molecular methods used to study genetic variation will offer an entry to this powerful set of modern tools.

In enzyme studies the tissues of organisms are generally mechanically homogenized and the resulting homogenate analyzed for the presence and kinds of enzymes. Generally, larger tissue samples are required for enzyme studies than for studies of DNA. Since DNA studies may be performed on very small samples, biologists may sample populations without damaging them. Nondestructive sampling is especially important in the study of endangered species or in any study following known individuals over long periods of time. For instance, the grizzly bears of Glacier National Park are being counted and mapped using the DNA in hair that the bears leave on scratching trees and on baited hair traps (USGS 2000). To obtain sufficient quantities of DNA for analysis, such as that contained within a hair follicle, biologists generally use one of two techniques to amplify the quantity of DNA present in a sample. DNA is usually cloned either by using bacteria and recombinant DNA technology or by a procedure called polymerase chain reaction or PCR (Hillis et al. 1996). During the PCR process, short, single-stranded DNA is used as primers for DNA synthesis. Each primer is highly specific for a given nucleotide sequence and can be used to amplify a specific locus or gene. However in one approach, designed simply to identify genetic differences or similarities, somewhat randomly chosen primers are used to amplify unspecified DNA sequences. This is the so-called random amplified polymorphic DNA, or RAPD, method. These techniques are well presented in

many introductory biology texts.

Once a sufficient quantity of DNA has been obtained, the sample may be analyzed in several ways. One commonly applied method uses **restriction enzymes**, enzymes produced naturally by bacteria to cut up foreign DNA. Restriction enzymes cut DNA molecules at particular places called **restriction sites**. The locations of restriction sites along a DNA molecule are determined by the locations of specific **nucleotide** sequences. Nucleotides are the basic building blocks of nucleic

acids and are made up of a five-carbon sugar (deoxyribose or ribose), a phosphate group, and a nitrogenous base (guanine, cytosine, adenine, or thymine). The nucleotide sequences determining restriction sites along the length of a DNA molecule are different for different restriction enzymes. Because restriction sites are determined by a specific sequence of base pairs on the DNA molecule, differences in number and location of restriction sites reflect differences in DNA structure. When exposed to a particular restriction enzyme, a given DNA molecule will be broken up into a series of DNA fragments of precise number and lengths. The number and lengths of DNA fragments, called restriction fragments, are determined by the number and location of restriction sites for a particular restriction enzyme. Therefore, if DNA samples from different organisms exposed to the same restriction enzyme yield different numbers and lengths of DNA fragments, we can conclude that those organisms differ genetically.

The number and sizes of restriction fragments resulting from treating a DNA molecule with restriction enzymes or the number of isozymes present in the homogenized tissues of an organism may be analyzed using a technique called **electrophoresis.** Electrophoresis uses the rate at which enzymes, DNA fragments, or other macromolecules

move in an electrical field as a means of identifying the molecules (fig. 8.27). When placed in an electrical field, a molecule will move either toward the positive or negative end of the field. Negatively charged molecules will move toward the positive end, while positively charged molecules will move toward the negative pole. Smaller molecules move more rapidly than larger molecules. Due to the influences of molecule size and charge on rates of movement, isozymes or DNA restriction fragments of different structure will migrate at different rates during electrophoresis. Consequently during a given time interval, molecules of different sizes will migrate different distances from the point where they are initially placed in the electrical field.

Electrophoresis is generally referred to as gel electrophoresis because migration of molecules generally takes place in one of several possible types of gels. Various stains and other techniques have been developed to detect the locations of DNA fragments or of specific enzymes within the gel after an electrophoresis run. The result is a pattern of banding in a gel that



Figure 8.27 Gel electrophoresis can be used to study genetic variation.

generally allows the biologist to identify genetic differences among individuals. By sampling many individuals from a population researchers can characterize the genetic structure of the population and determine if populations differ genetically.

What do the banding patterns, such as those shown in figure 8.27, reveal about the genetics of individuals and populations? We can say that the sample of four hypothetical individuals depicted in figure 8.27 includes three different genotypes. Individuals I and II have the same genotype, while individuals III and IV are of two other genotypes. By sampling many individuals and many enzyme systems or genetic loci in a population, the biologist will be able to estimate the genetic variation and genetic composition of a population. After characterizing several populations, we can test questions such as whether population size influences genetic variation in species such as the Chihuahua spruce (see fig. 8.21) or whether island populations of a species have less genetic variation than mainland populations of the same species (see fig. 8.23).

An approach that gives a very high resolution picture of the genetic makeup of individuals and populations and that is receiving increasing attention is **DNA sequencing.** Because sequencing reveals the sequence of nucleic acids along DNA molecules, this tool gives the ultimate genetic information. The number of DNA sequences described is increasing rapidly and our ability to interpret and compare DNA sequence data is also increasing at an impressive rate (Hillis et al. 1996). While the human genome project has assumed center stage (DOE 2000), the genomes of many other species are completely described or will be soon.

David Hillis and his coauthors (1996) suggest that DNA sequencing can be used as a powerful tool for studying genetic variation within and among populations. Some of the areas where sequencing might be applied include geographic variation among populations and gene flow among popula-

tions. However, Hillis and his team point out that there are trade-offs. Obtaining and interpreting the highly detailed information provided by sequencing for one or two loci necessarily limits the number of loci that the biologist can study. Where the emphasis is on studying larger numbers of loci, isozyme studies or restriction fragment analyses allow the researcher to study larger numbers of loci. At this point in time, the biologist's choice of methods is governed by these trade-offs.

Future advances in DNA sequencing and analysis will very likely improve the potential for comparing large numbers of loci using sequence data. Regardless of future development, ecologists now have many powerful tools for assessing the extent of genetic variation in populations. These tools will be invaluable as this generation of ecologists works to conserve the earth's biodiversity.

SUMMARY

Darwin and Mendel complemented each other well and their twin visions of the natural world revolutionized biology. The synthesis of the theory of natural selection and genetics gave rise to modern evolutionary ecology. Here we examine five major concepts within the area of population genetics and natural selection.

Phenotypic variation among individuals in a population results from the combined effects of genes and environment. The first biologists to conduct thorough studies of phenotypic and genotypic variation and to incorporate experiments in their studies, focused on plants. Clausen, Keck, and Hiesey explored the extent and sources of morphological variation in plant populations, including both the influences of environment and genetics. Case determined that the best predictor of chuckwalla, *Sauromalus*, body length was average winter rainfall. Tracy's laboratory growth experiments indicated that variation in body size among chuckwalla populations is at least partly determined by genetic differences among populations.

The Hardy-Weinberg equilibrium model helps identify evolutionary forces that can change gene frequencies in populations. Because evolution involves changes in gene frequencies in a population, a thorough understanding of evolution must include the area of genetics known as population genetics. One of the most fundamental concepts in population genetics, the Hardy-Weinberg principle, states that in a population mating at random in the absence of evolutionary forces, allele frequencies will remain constant. For a population in Hardy-Weinberg equilibrium in a situation where there are only two alleles at a particular locus, p + q = 1.0. The frequency of genotypes in a population in Hardy-Weinberg equilibrium can be calculated as $(p + q)^2 = (p + q) \times (p + q) = p^2 + q^2$ $2pq + q^2 = 1.0$. The conditions necessary to maintain constant allele frequencies in a population are: (1) random mating, (2) no mutations, (3) large population size, (4) no immigration, and (5) equal survival and reproductive rates for all genotypes. When a population is not in Hardy-Weinberg equilibrium, the Hardy-Weinberg principle helps us to identify the evolutionary forces that may be in play.

Natural selection is the result of differences in survival and reproduction among phenotypes. Natural selection can lead to change in populations but it can also serve as a conservative force, impeding change in a population. Stabilizing selection acts against extreme phenotypes and as a consequence, favors the average phenotype. By favoring the average phenotype, stabilizing selection decreases phenotypic diversity in populations. Directional selection favors an extreme phenotype over other phenotypes in the population. Under directional selection, the average of the trait under selection can change over time. Disruptive selection favors two or more extreme phenotypes over the average phenotype in a population, leading to a increase in phenotypic diversity in the population.

The extent to which phenotypic variation is due to genetic variation determines the potential for evolution by natural selection. The most general postulate of the theory of natural selection is that the environment determines the evolution of the anatomy, physiology, and behavior of organisms. Some of the clearest demonstrations of natural selection have resulted from studies of populations of Galápagos finches. Losos, Warheit, and Schoener used replicated field experiments to study natural selection for changes in morphology in *Anolis* lizard populations. Their results indicate that colonizing populations can adapt rapidly to new environmental con-

ditions. Studies by Carroll and several colleagues show that soapberry bug populations living on native and introduced host plants have undergone natural selection for traits that favor their survival and reproduction on particular host plant species. Hundreds of other examples of natural selection have been brought to light during the nearly one and a half century since Darwin published his theory. Still, evolutionary ecology remains a vigorous field of inquiry with plenty of debate, selfcriticism, and significant work yet to be done.

The earlier research on adaptation of populations to local environmental conditions used transplant experiments to detect genetic differences among populations. More recent research on genetic variation within and among populations has applied techniques developed in molecular biology. Ecologists now have many powerful tools, ranging from classical techniques to modern technologically sophisticated approaches, for assessing the extent of genetic variation within and among populations and meeting the challenge of documenting and conserving biodiversity.

Random processes, such as genetic drift, can change gene frequencies in populations, especially in small populations. Genetic drift is theoretically most effective at changing gene frequencies in small populations such as those that inhabit islands. One of the greatest concerns associated with fragmentation of natural ecosystems due to human land use is that reducing habitat availability will decrease the size of animal and plant populations to the point where genetic drift will reduce the genetic diversity within natural populations. Ledig and his colleagues found a significant positive correlation between population size and genetic diversity in populations of Chihuahua spruce, a naturally fragmented population of trees living on mountain islands. Frankham showed that compared to mainland populations, island populations generally include less genetic variation. Saccheri and his colleagues found that higher heterozygosity (genetic diversity) was associated with lower rates of population extinction through the effects of heterozygosity on larval survival, adult longevity, and egg hatching in populations of the Glanville fritillary butterfly, Melitaea cinxia.

Review Questions

- 1. Contrast the approaches of Charles Darwin and Gregor Mendel to the study of populations. What were Darwin's main discoveries? What were Mendel's main discoveries? How did the studies of Darwin and Mendel prepare the way for the later studies reviewed in chapter 8?
- 2. Review the historical studies of genetic and phenotypic variation among populations of plants using transplant experiments. How did the studies of Clausen, Keck, and Hiesey complement these earlier studies?
- 3. What environmental variable did Ted Case determine to be the best predictor of variation in body size among populations of chuckwallas? Did Case's studies of chuckwallas demonstrate genetic differences among his study populations? What did the more recent studies by Christopher Tracy add to our understanding of variation among chuckwalla populations?
- 4. What is the Hardy-Weinberg principle? What is Hardy-Weinberg equilibrium? What conditions are required for Hardy-Weinberg equilibrium?
- 5. Review the Hardy-Weinberg equilibrium equation. What parts of the equation represent gene frequencies? What elements represent genotype frequencies and phenotype frequencies? Are genotype and phenotype frequencies always the same? Use a hypothetical population to specify alleles and allelic frequencies as you develop your presentation.

- 6. What is genetic drift? Under what circumstances do you expect genetic drift to occur? Under what circumstances is genetic drift unlikely to be important? Does genetic drift increase or decrease genetic variation in populations.
- 7. Suppose you are a director of a captive breeding program for a rare species of animal, such as Siberian tigers, that are found in many zoos around the world but are increasingly rare in the wild. Design a breeding program that will reduce the possibility of genetic drift in captive populations.
- 8. Jonathan Losos, Kenneth Warheit, and Thomas Schoener's studies of *Anolis* populations demonstrated significant morphological change following introduction of the lizards to various islands differing in vegetative structure. Design an experiment to determine whether the morphological changes in the study populations were based on genetic changes. Can you adapt the methods of Christopher Tracy to this project?
- 9. How did the studies of Scott Carroll and his colleagues demonstrate rapid evolutionary adaptation to introduced soapberry plants? What advantages do a group of organisms, such as soapberry bugs, offer to researchers studying natural selection compared to larger organisms such as Chihuahua pines and chuckwalla lizards?
- 10. How do classical approaches to genetic studies, such as common garden experiments, and modern molecular techniques, such as DNA sequencing, complement each other? What are the advantages and disadvantages of each?

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