

# Adaptation to Life in Varying Environments

Adaptation results from natural selection on traits that affect evolutionary fitness

The phenotype is the expression of the genotype in the form and function of the individual organism

Each type of organism has an activity space defined by conditions of the environment

Organisms can select microhabitats

Acclimation is a reversible change in structure in response to environmental change

Developmental responses are irreversible changes in response to persistent variation in the environment

Migration, storage, and dormancy enable organisms to survive extreme conditions

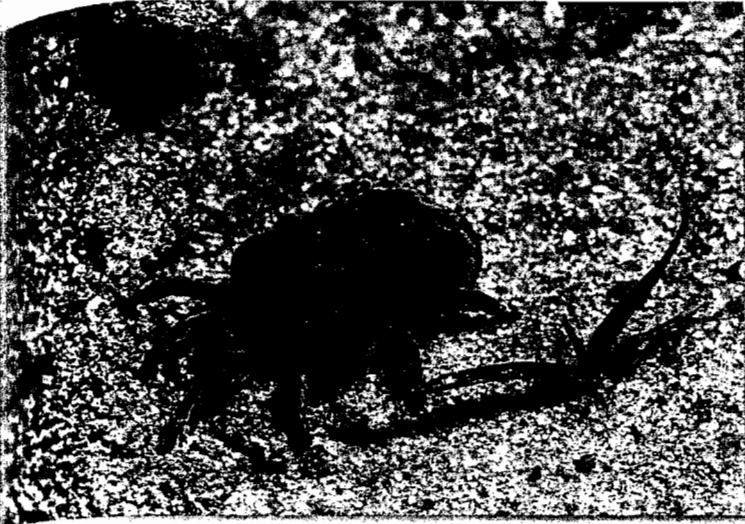
Animals forage in a manner that maximizes their fitness



The Mojave Desert of southern California has a climate with little rain, searing summer heat, and chilling winter cold. These conditions are so forbidding that, except for a few struggling plants, the desert appears nearly

devoid of life for most of the year. But the desert's silence is occasionally broken during the milder days of winter by swarms of insects and other creatures that appear on the surface or fly above it for a few hours, and then disappear as mysteriously as they came. One of the more conspicuous of these creatures is the giant red velvet mite (■ Figure 9.1).

Several decades ago, biologists Lloyd Tevis and Irwin Newell began a study of the behavior of the giant red velvet mite in relation to the physical conditions of its environment. They found that the mites spend most of the year in burrows dug in the sand. The particular conditions that favor the emergence of mites occur infrequently in the Mojave Desert. During four years of observation, adults appeared aboveground only ten times, always during the cooler months of December, January, or February, when they can tolerate the temperatures on the desert's surface. An individual mite appeared only once each year. Tevis and Newell could predict from their observations that an emergence would occur on the first sunny day after a rain of more than 8 millimeters, provided that air temperatures were moderate. On the day of a major emergence, the mites came out of their burrows between 9:00 and 10:00 A.M., and by late morning one could find thousands of mites scurrying across the desert sands in all directions. At midday, between 11:30 and 12:30, the mites dug back into the sand, not to emerge again until the following year.

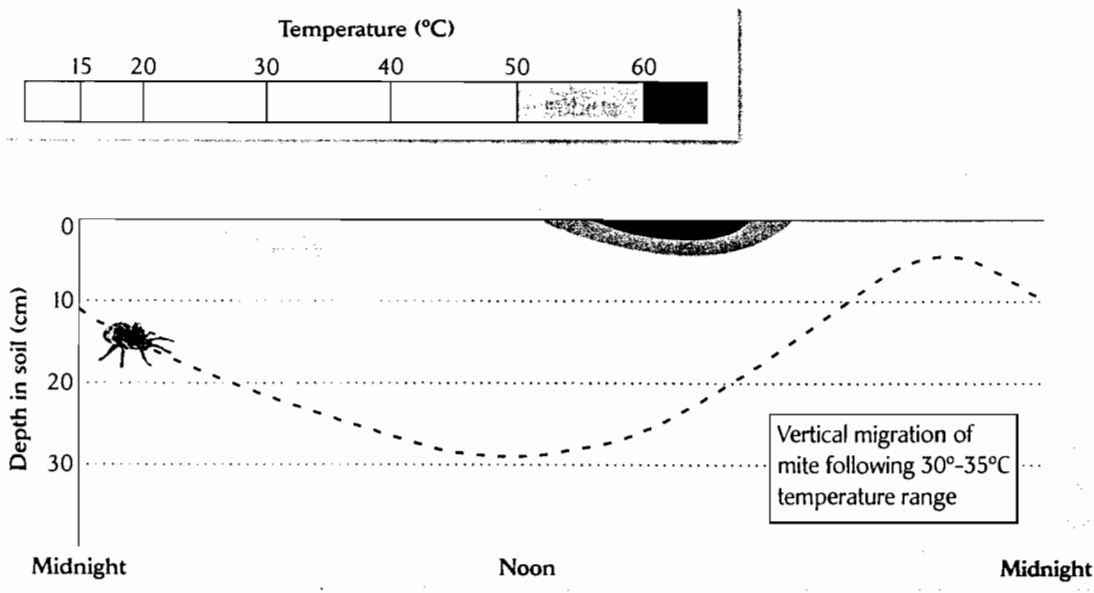


■ **Figure 9.1** The giant red velvet mite lives in a stressful desert environment. An adult mite is shown on the surface of the ground close to its burrow, within which it spends all but a few hours of its life. Photo by P. Ward/Bruce Coleman.

During its 2- to 3-hour stay above ground each year, each mite must perform two important functions: feeding and mating. The mites feed on termites, which appear on the same day the mites emerge, flying in

large swarms over the desert sand, their own emergence presumably triggered by the same physical cues that urge the mites to leave their burrows. Because mites cannot fly, they can feed only after the termites have dropped to the ground and shed their wings, but before they have burrowed into the sand to form new colonies. If a mite feeds successfully during this narrow window of opportunity, it soon mates and prepares to re-enter the sand itself.

About midday, after the mites have fed and mated, they congregate in troughs on the windward sides of sand dunes, where surface temperature and the size of the sand particles are "just right" (less than half a millimeter in diameter). Here they re-enter the sand almost simultaneously. The mites continue digging their new burrows until the coolness of the late winter afternoon slows their activity. Burrowing continues on subsequent days when the sand becomes warm enough, until the burrows are completed. During the rest of the year, the adult mite spends its time moving up and down in its burrow to follow the movement of its preferred temperature zone as the surface of the sand heats and cools each day (■ Figure 9.2).



■ **Figure 9.2** The giant red velvet mite must adjust to changing environmental conditions. The vertical migration of a mite in its burrow follows changes in soil temperature throughout the course of a typical summer day.

The red velvet mite's world is extremely variable in time and space. Rain comes sporadically. Desert temperatures vary between day and night extremes almost as much as between summer and winter. The mite's world is so forbidding that an individual can be active in only a small portion of its environment, or for only a very limited amount of time. Indeed, all organisms—except, perhaps, for those living at great depths in the seas and in the farthest reaches of caves—must cope with a varied and constantly changing environment. Organisms that can adjust to these changes have the best possible chance of surviving and producing offspring for the next generation.

Each response of an organism to a change in its environment affects the number of descendants it leaves in future populations. Individuals that make the “wrong” response are more likely to die or fail to reproduce than those that respond appropriately. Of course, what is “right” or “wrong” depends on the qualities of the organism and its particular ecological circumstances. For example, whether a sparrow should store fat during times of food abundance depends on whether it is likely to need energy reserves in the near future for a long-distance migration, or as insurance to carry it through a spell of bad weather. In the absence of such need, extra fat is disadvantageous because it reduces speed and maneuverability and increases risk of predation.

In the course of this chapter, we shall learn how different kinds of environmental variation demand different adaptations of individuals. Some kinds of variation occur over space, in which case an organism can make choices about where to live. Other kinds of variation occur over time and are unavoidable; each individual, or its lineage, must be able to survive all the extremes of the environment to persist. Because most of the traits organisms possess have evolved in response to the particular environments in which they live, we shall begin our discussion of adaptation to life in varied and varying environments with a brief explanation of some important aspects of evolution.



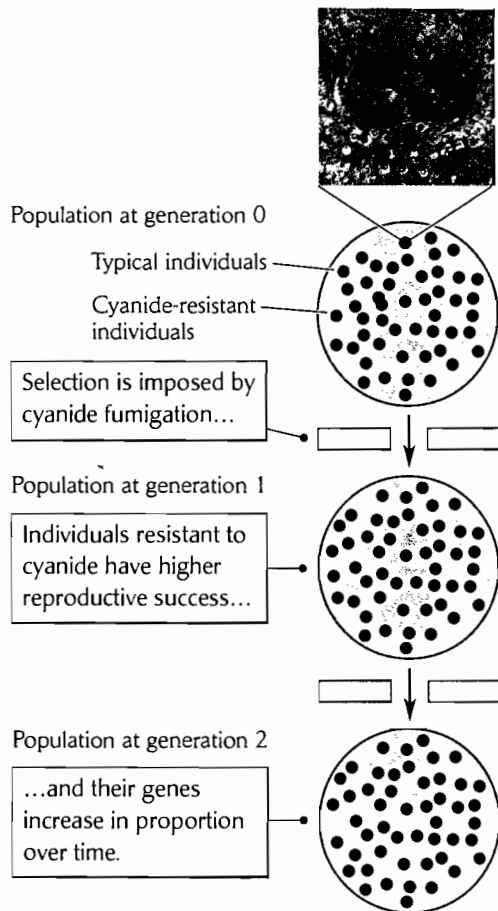
### Adaptation results from natural selection on traits that affect evolutionary fitness

Each individual in a sexually reproducing population is endowed with a unique genetic constitution, or **genotype**, made up of a combination of genes from its mother and its father. Such genetic variability within a population has many consequences, the most important of which for the study of ecology is evolution by natural selection. The term **evolution** pertains to any change in the genetic

makeup of a population. When genetic factors cause differences in fecundity and survival among individuals, evolutionary change comes about through **natural selection**. Individuals whose attributes enable them to achieve higher rates of reproduction leave more descendants, and therefore the genes responsible for these attributes increase in the population. The reproductive success of an individual is referred to as its evolutionary **fitness**.

Consider how these principles apply in the following example of evolutionary change in a California citrus pest. Early in the twentieth century, certain species of scale insects were serious pests in citrus orchards in southern California. An effective means of controlling scale populations was to fumigate orchards with cyanide gas. However, after several years of such treatment, the gas killed fewer of the insects, and before long the scale regained its pest status. Researchers determined that scale insects had evolved a genetically based resistance to cyanide poisoning. Furthermore, when they surveyed orchards in areas that had never been fumigated, they found that small numbers of individuals possessed an innate resistance to cyanide. Thus, despite their initial successes, fumigation programs in the end had favored reproduction by cyanide-resistant individuals, whose progeny then increased to epidemic proportions (■ Figure 9.3). The citrus scale story illustrates the three main ingredients of evolution by natural selection: (1) variation among individuals, (2) inheritance of that variation (the genetic basis of evolution), and (3) differences in reproductive success, or fitness, related to genetic variation.

Most evolutionary biologists believe that the diversification of living beings over the long history of life has been guided primarily by natural selection. It is important to understand, however, that natural selection is not an external force that urges organisms toward some predetermined goal, in the sense that humans artificially “select” cows to achieve a higher rate of milk production in their herds. Quite the opposite. Selection occurs because of differences in reproductive success among individuals endowed with different form or function in a particular environment. The process that creates selection is ecological—namely, the interaction of individuals with their environment, including its physical conditions, food resources, predators, and so on. A cold winter wind doesn't care whether a bird is well insulated by its plumage. Whether a rabbit runs fast or not is irrelevant to evolution. All that matters is whether fast rabbits leave more offspring, perhaps because they are more likely to escape foxes. One presumes that a fox would prefer to chase slow rabbits, but, alas, by catching slow ones, it ends up favoring reproduction by faster ones.



**Figure 9.3** Evolutionary change in a population may result from a change in the environment. Genes that confer resistance to cyanide are present at low frequencies in populations of scale insects that have never been exposed to cyanide, simply because of recurrent mutations. In the absence of cyanide, the trait may actually be mildly harmful. When populations are fumigated on a regular basis, however, the gene for cyanide resistance confers high fitness, and its frequency in populations rapidly rises. Photo by Jack Kelly Clark, courtesy of the University of California Statewide IPM Project.



### The phenotype is the expression of the genotype in the form and function of the individual organism

Each individual's genotype includes all of its genes. The outward expression of its genotype, called the **phenotype**, is its structure and function. Thus, a genotype is a set of genetic instructions, and a phenotype is the rendering, or expression, of a genotype in the form of an organism. Of course, the environment also influences this rendering. To

put it another way, the genotype is to the phenotype as blueprints are to the structure of a building. In this analogy, the effects of environmental influences are like details in a blueprint that are left up to the discretion of the building contractor, which may hinge, for example, on unpredictable changes in the availability of certain construction materials.

Most genes encode a particular protein, which may be used as part of an organism's structure or may function as an enzyme or hormone. Different forms of a particular gene are referred to as **alleles**. In many cases, alleles create perceptible and measurable differences in an organism's phenotype. For example, blue-eyed and brown-eyed humans have different alleles of a single gene, which controls one of the pigment systems that determines eye color. Many genetic disorders, such as sickle-cell anemia, Tay-Sachs disease, cystic fibrosis, and albinism, as well as tendencies to develop certain cancers and Alzheimer's disease, are caused by defective alleles of individual genes.

Every individual has two copies of each gene, one inherited from its mother and one from its father (exceptions include sex-linked genes and organisms that reproduce without the sexual union of gametes). An individual that has two different alleles of a particular gene is said to be **heterozygous** for that gene. When both copies of a gene are the same, that individual is **homozygous**. When an individual is heterozygous, the two different alleles may produce an intermediate phenotype, or one may mask the expression of the other. In the latter case, one allele is said to be **dominant** and the other **recessive**. When heterozygotes have an intermediate phenotype, the alleles are said to be **codominant**. Most harmful alleles are recessive, and the normal gene product of the dominant allele masks the defective function of their gene products in heterozygous individuals.

While all phenotypic traits have a genetic basis, they are also influenced by variations in the environment, either through the effects of environmental conditions on individuals (as in the effect of food supply on growth and development) or through the responses of individuals to variation in their environments. Such environmentally induced variation in the phenotype is referred to as **phenotypic plasticity**. The capacity of an individual to exhibit different responses to its environment may itself be an evolved trait. That is, the way in which the individual responds to environmental variation is also subject to evolution by natural selection. We shall look at phenotypic plasticity in more detail in the next chapter, but let us keep in mind the difference between these plastic responses by individuals and evolutionary responses by populations as we consider the relationship of organisms to their environments.



## Each type of organism has an activity space defined by conditions of the environment

Each organism functions best within a limited range of conditions, which we may refer to as its **activity space**. This concept applies to all aspects of an individual's life, whether it is literally active or not; here we may think of "activity" as synonymous with "performance." For some environmental factors, the activity of individual organisms tends to be highest within a relatively narrow range (■ Figure 9.4). Activity might be measured as rate of photosynthesis, survival, or swimming speed, all of which influence an individual's reproductive success in some way. The environmental factor might be temperature, soil acidity, nutritional quality of food items, or structure of the foraging substrate. Away from the optimum conditions, activity decreases, and consequently so does the individual's probability of surviving and ability to produce offspring. Close to the optimum conditions, reproductive success is high enough to maintain a population. Under marginal conditions, an individual might be able to maintain itself indefinitely, but not replace itself in future populations. Extreme conditions are unsuitable for individual maintenance, and an individual can venture into such conditions only for short periods.



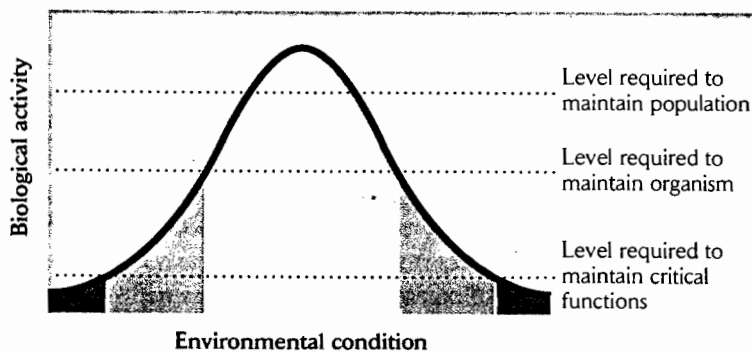
## Organisms can select microhabitats

Plants have relatively little choice as to where they live, even though, as we have seen, roots can "forage" for high concentrations of soil minerals, growing shoots can seek

out light gaps, and wind, water, and animal dispersers may distribute plant seeds nonrandomly through the environment. Unlike plants, most animals have freedom to move about the environment and choose a habitat in which to live. Nonetheless, even within a habitat, there are distinct differences in temperature, moisture, salinity, and other factors. Parts of the environment that can be distinguished by their conditions are referred to as **microhabitats** or **microenvironments**. In deserts, for example, the shaded ground under a shrub is often cooler and moister than surrounding areas exposed to direct sunlight, although clearly these conditions vary through the course of the daily cycle and with the seasons.

Responses of animals to the changing array of microhabitats in their environments can be illustrated by the diurnal behavioral cycles of lizards. Although lizards do not regulate their body temperatures by generating heat metabolically, they do take advantage of solar radiation and warm surfaces to maintain their temperatures within a suitable range during the day. Thus, it is not surprising that lizards respond to the temperatures of different microhabitats. At night, external sources of heat disappear, and the lizard's body temperature gradually drops to that of the surrounding air.

The desert iguana (*Dipsosaurus dorsalis*) of the southwestern United States lives in a severe environment. Shade temperatures can reach 45°C in summer and plunge below freezing in winter. Desert iguanas have a preferred body temperature range of 39°–43°C. During mid-July, the thermal environment changes rapidly between day and night extremes. Desert iguanas can move about the desert surface in search of food and remain within their preferred range for only about 45 minutes in mid-morning and a similar period in the early evening (■ Figure 9.5). During the remainder of the day, they seek the shade of plants or the coolness of their burrows, where temperatures rarely exceed their preferred range. At night,



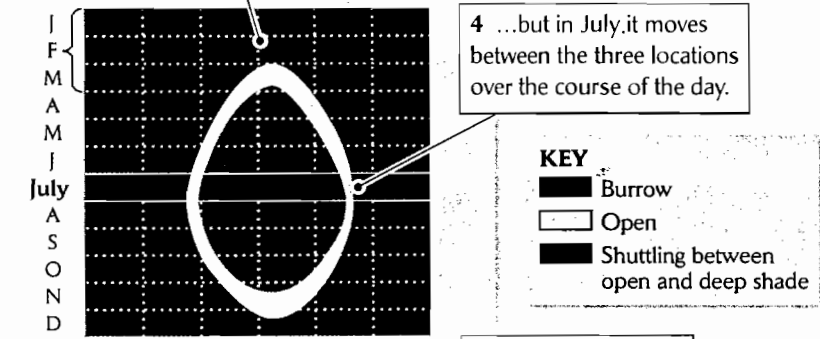
■ **Figure 9.4** Biological activity is related to environmental conditions. For some environmental factors, the activity of individual organisms is sufficient to maintain a population only within a narrow intermediate range. Organisms can maintain themselves for long periods over a broader range of conditions and briefly over a yet broader range.

1 The desert iguana regulates its body temperature by basking in the sun...

2 ...or retreating to deep shade or its burrow.

3 The time spent in each location varies at different times of the year. January through March the iguana stays in its burrow...

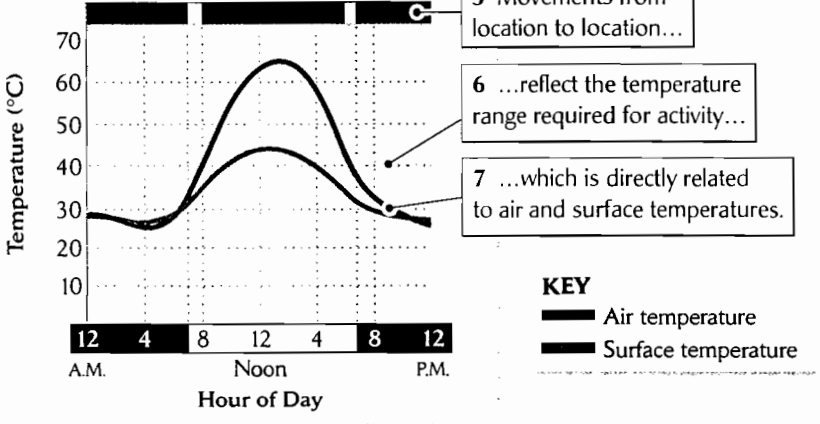
4 ...but in July, it moves between the three locations over the course of the day.



5 Movements from location to location...

6 ...reflect the temperature range required for activity...

7 ...which is directly related to air and surface temperatures.



**Figure 9.5** The desert iguana regulates its body temperature by microhabitat selection. The activity space of the desert iguana (*Dipsosaurus dorsalis*) within its habitat in southern California is shown over the entire year and over a summer day (July 15). After W. A. Beckman, J. W. Mitchell, and W. P. Porter, *J. Heat Transfer* (May 1973):257–262.

desert iguanas retreat to the safety of their burrows. If an iguana were to remain aboveground in the cool evening air, its body temperature would drop rapidly and it would become too sluggish to escape predators.

Winter cold restricts *Dipsosaurus* to brief periods of activity in the middle of the day, when air temperatures rise to the point at which individuals can come aboveground and forage. Between early December and the end of February, most days are so cold that desert iguanas cannot even venture from their burrows. Spring offers more favorable temperatures for iguanas. In May, individuals forage actively on the ground surface for a businesslike 9:00 A.M. to 5:00 P.M., only occasionally seeking the cool shade of plants.

**ECOLOGISTS IN THE FIELD**



*Temperature and microhabitat selection by the cactus wren*

Unlike the desert iguana, the cactus wren (Figure 9.6), an insectivorous bird that lives in deserts of the southwestern United States and northern Mexico, maintains a constant body temperature. However, because the wren has no source of free water, it must avoid gaining too much heat from its environment. Otherwise, it would have to dissipate excess body heat by the cooling effect of evaporation from its respiratory tract (see Chapter 2).



■ **Figure 9.6** The cactus wren (*Campylorhynchus brunneicapillus*) is a conspicuous resident of deserts in the southwestern United States and northern Mexico. Photo by Craig K. Lorenz/Photo Researchers.

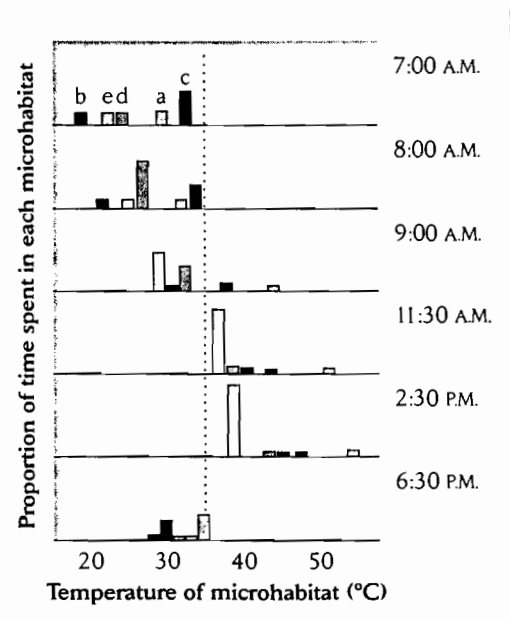
Thus, the wren's activity space, like that of the desert iguana, reflects changes in environmental conditions throughout the day and season.

Observations made by Robert E. Ricklefs and F. Reed Hainsworth in deserts near Tucson, Arizona, showed that cactus wrens seek favorable microhabitats within which to feed as the thermal environment changes throughout the day. During cool early mornings, wrens forage throughout most of the environment, searching for food among foliage and on the ground. As the day brings warmer temperatures, wrens select cooler parts of their habitat, particularly the shade of small trees and large shrubs, always managing to avoid feeding where the temperature exceeds 35°C (■ Figure 9.7). When the minimum temperature in the environment rises above 35°C, at which point birds must use evaporative cooling to maintain their body temperatures even when inactive, the wrens stop feeding and perch quietly in deep shade.

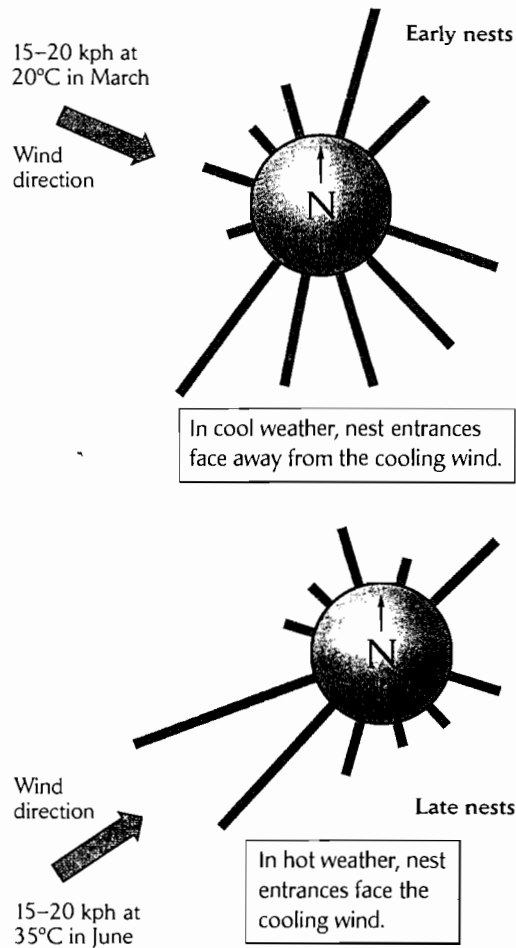
Although an adult cactus wren can move without restraint to any part of its habitat, its nest is fixed in place: wren chicks cannot move among microhabitats until they are old enough to leave the nest. The microenvironment of the nest must therefore be within the tolerance range of chicks at all times. Cactus wrens appear to achieve this both by choosing particular nest sites and by orienting their nests in particular directions. Cactus wrens build untidy, enclosed nests—bulky, somewhat haphazardly constructed balls of grass—with side entrances. Once a nest is built, of

course, its position and orientation cannot be changed. For a month and a half, from the first egg until the young fly off, the nest must provide a suitable environment day and night, in hot and cool weather.

During the long breeding period (March through September) in southern Arizona, cactus wrens usually rear several broods of young. Early in spring, they build their nests so that the entrances face away from the direction of the cold winds; during the hot summer months, they orient their nests to face prevailing afternoon breezes, which circulate air through the nest chamber and facilitate heat loss (■ Figure 9.8). This strategy makes a difference! Nests ori-



■ **Figure 9.7** Temperature affects microhabitat use by cactus wrens. Microhabitat use is shown over the course of a day in late spring. Microhabitats vary in degree of thermal stress between exposed ground (a) and the deep shade of trees (e). From R. E. Ricklefs and F. R. Hainsworth, *Ecology* 49:227–233 (1968). Photo by R. E. Ricklefs.



■ **Figure 9.8** The orientation of cactus wren nest entrances changes during the breeding season. Lengths of bars represent relative numbers of nests with each orientation. After R. E. Ricklefs and F. R. Hainsworth, *Condor* 71:32–37 (1969).

ented properly for the season are consistently more successful (82% produce viable offspring) than nests facing in the wrong direction (only 45% are successful).



### Acclimation is a reversible change in structure in response to environmental change

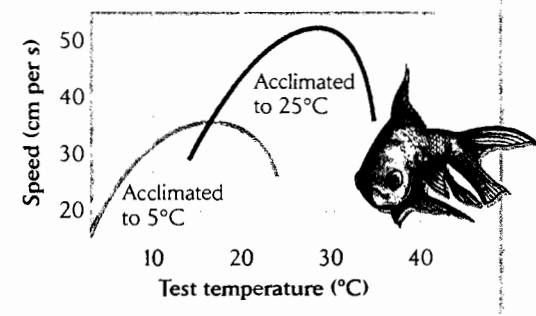
Growing thicker fur in winter, producing smaller leaves during the dry season, increasing the number of red cells in the blood at high altitude, and producing enzymes with different temperature optima or lipids that remain fluid at different temperatures are all forms of **acclimation**. Acclimation may be thought of as a shift in the range of physiological tolerances of the individual. Because these changes involve modifications of the body's structure and metabolic machinery, they require days to weeks. Thus, acclima-

tion is a strategy restricted to seasonal and other persistent variations in conditions. Acclimation is reversible, and allows organisms to follow the ups and downs of their environments. As long as the environmental change is persistent, it is a good strategy. However, increased tolerance of one extreme often brings reduced tolerance of the other.

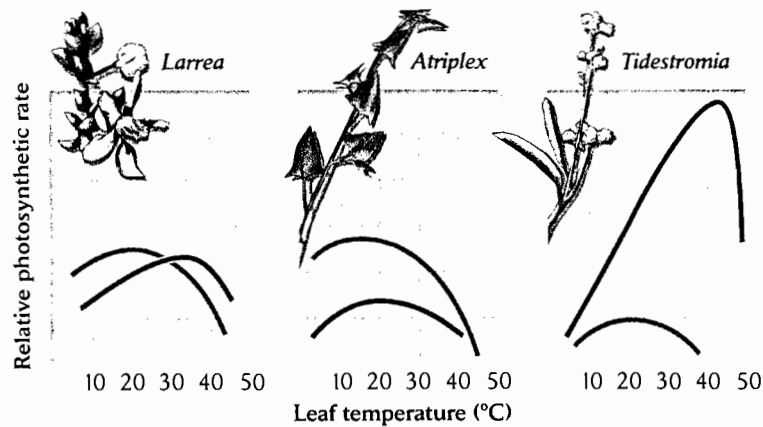
By producing enzymes and other molecules having different temperature optima, a cold-blooded (poikilothermic) animal can adjust its activity space in response to prevailing environmental conditions. The relationship between the swimming speed of goldfish and water temperature shows both the advantages and the limitations of acclimation. Goldfish swim most rapidly when acclimated to 25°C and placed in water between 25° and 30°C, conditions that closely resemble those of their natural habitat (■ Figure 9.9). Lowering the acclimation temperature to 5°C increases the swimming speed at 15°C, but reduces it at 25°C.

An organism's capacity for acclimation often reflects the range of conditions experienced in its natural environment. *Larrea divaricata* (creosote bush) inhabits interior deserts in western North America and maintains photosynthetic activity during the cool winters as well as the hot summers. Measurements of the rate of photosynthesis in this plant show a shift in the temperature optimum characteristic of thermal acclimation. Specifically, photosynthetic rate reaches the same level in plants grown at 20°C and 45°C, but plants grown at 20°C do not perform as well at 45°C as plants acclimated to that temperature. The basis for this acclimation seems to be changes in the viscosity of membranes directly related to photosynthetic pathways.

Where the environment normally is relatively constant, we would not expect organisms to have evolved the ability to respond strongly to environmental variation or to tolerate conditions that differ from the norm. Evolution favors



■ **Figure 9.9** Acclimation can shift an organism's activity space in response to environmental conditions. Swimming speed as a function of temperature is shown for goldfish acclimated to 5°C and to 25°C. After F. E. J. Fry and J. S. Hart. *J. Fish. Res. Bd. Can.* 7:169–174 (1948).



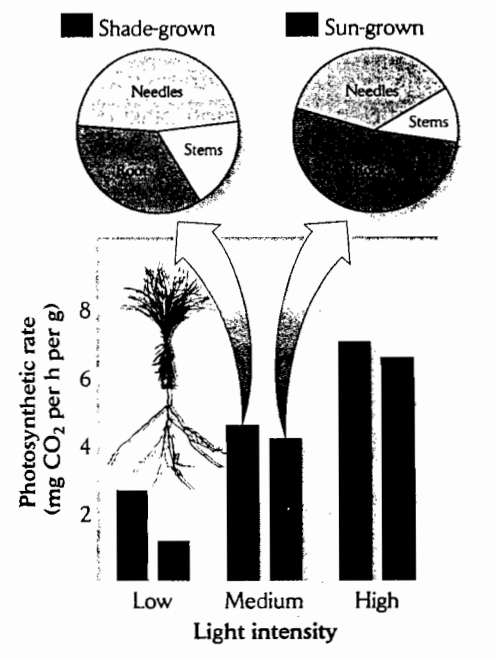
■ **Figure 9.10** The capacity for acclimation may reflect the range of conditions in the environment. Photosynthetic rate as a function of leaf temperature is shown for three species of plants (genera *Larrea*, *Atriplex*, and *Tidestromia*) grown under moderate (blue line) and hot temperatures (red line). From P. W. Hochachka and G. N. Somero, *Biochemical Adaptation*, Princeton University Press, Princeton, NJ (1984); after O. Bjorkman, M. R. Badger, and P. A. Arnold, in N. C. Turner and P. J. Kramer (eds.), *Adaptation of Plants to Water and High Temperature Stress*, Wiley, New York (1980), pp. 231–249.

economical designs, and we presume that the capacity to respond to environmental change imposes a cost for the organism. That these mechanisms have been dispensed with when plants experience only narrow ranges of temperatures is shown by the photosynthetic rates of two other plants from western North America. *Atriplex glabriuscula* is a species of saltbush native to cool coastal regions of California, where temperatures during the growing season rarely exceed 20°C. Unlike *Larrea*, *Atriplex* does not increase its photosynthetic rate at high temperatures when acclimated to 40°C, although it may respond in other ways. However, whatever physiological changes that do occur during acclimation to high temperature cause saltbush plants to perform less well at lower temperatures (■ Figure 9.10). In contrast, the thermophilic (heat-loving) species *Tidestromia oblongifolia* cannot acclimate to cool temperatures. Photosynthesis is reduced uniformly over a wide range of leaf temperatures from 10°C to 40°C when plants are maintained for long periods in cool temperatures. The responses of *Atriplex* to growing under hot temperatures and of *Tidestromia* to growing under cool temperatures appear to be generalized stress responses that allow individuals to survive under extreme conditions, rather than mechanisms that effectively broaden their activity spaces.

### Developmental responses are irreversible changes in response to persistent variation in the environment

Light intensity, among many other factors, influences the course of development in plants. Loblolly pine seedlings grown in shade have smaller root systems and more foliage than seedlings grown in full sunlight. Because a shaded environment taxes a plant's water economy less, shade-

grown seedlings can allocate more of their production to stem and needles; sun-grown seedlings develop more extensive root systems to obtain sufficient water. The larger proportion of foliage in a shade-grown seedling results in a higher rate of photosynthesis per unit of plant mass under given light conditions, particularly under low light intensities (■ Figure 9.11). These growth responses of pine seedlings show how plants allocate their production in such a



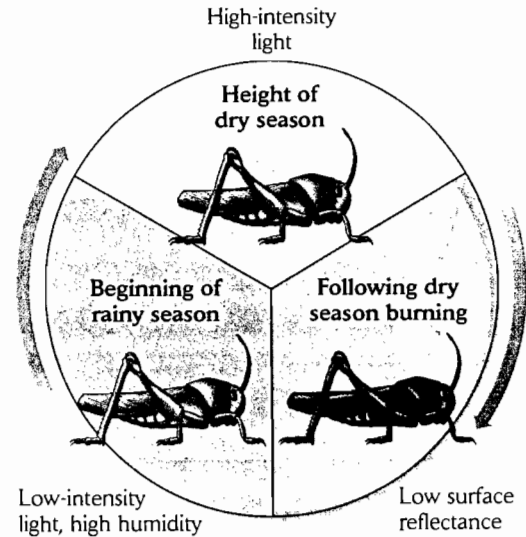
■ **Figure 9.11** Plants show developmental responses to light intensity. Distribution of dry matter and rates of photosynthesis are shown for loblolly pine (*Pinus taeda*) seedlings grown under shade and in full sunlight. After F. H. Bormann, in D. V. Thimann (ed.), *The Physiology of Forest Trees*, Ronald Press, New York (1958), pp. 197–215.

way as to acquire more of the resource that most limits their growth.

Another striking example of a developmental response is the coloration of several species of locusts and grasshoppers. It is important for the color of such insects to match the color of their backgrounds if they are to avoid detection by predators that use sight to locate prey. In tropical habitats with seasonal precipitation, the onset of the wet season stimulates the growth of lush, green vegetation. During the early part of the dry season this vegetation browns and dies, often exposing red-brown earth. As the seasonal drought intensifies, natural fires and those set by humans blacken the ground over vast areas. Consequently, there is a regular seasonal progression of color from green to brown to black and back to green again. Where this happens, many species of grasshoppers match the background coloration of the environment in which they develop (■ Figure 9.12).

The epidermis of the African grasshopper *Gastrimargus africanus* has a pigment system that permits any given area of skin to be either green or brown; both colors may occur on a single animal, but not in the same area of the body. The green and brown colors represent small biochemical variations on a single pigment molecule. In combination with brown, additional pigments may produce colors ranging from yellow through orange and red to black. Furthermore, black pigment (melanin) may be deposited in the cuticle that covers the epidermis. Between developmental stages a grasshopper sheds its epidermis, discarding its pattern of camouflaging coloration. A new layer of epidermis develops underneath, and thus a young grasshopper can change its color with each molt if the background color of its environment has changed in the meantime. Coloration in *Gastrimargus* responds to environmental conditions that are correlated with the color of its background, particularly quality and intensity of light, which are perceived by the eye and transmitted to the epidermis by hormones produced in the brain.

Developmental responses generally do not reverse themselves; once fixed during development, they remain unchanged for the rest of an individual's life (or particular developmental stage). Because of their long response times and irreversibility, developmental responses cannot accommodate short-term environmental changes. As a rule, therefore, only plants and animals in environments with persistent variation in the conditions experienced by different individuals exhibit developmental responses. Such organisms include plant species, such as loblolly pines, whose seeds may settle in many different kinds of habitats. In such cases, spatial rather than temporal heterogeneity in the environment may create the kind of persistent environmental variation that favors developmental



■ **Figure 9.12** Developmental responses can match organisms to environmental conditions. The epidermal coloration of the grasshopper *Gastrimargus africanus* responded to laboratory conditions designed to mimic light and humidity experienced during the wet season (green), the dry season (brown), and following burning (black). After C. H. Fraser Rowell, *Anti-locust Bull.* 47:1–48 (1970).

responses. Observed developmental responses generally match environmental change rather well, because individuals that respond inappropriately do not survive to produce descendants.

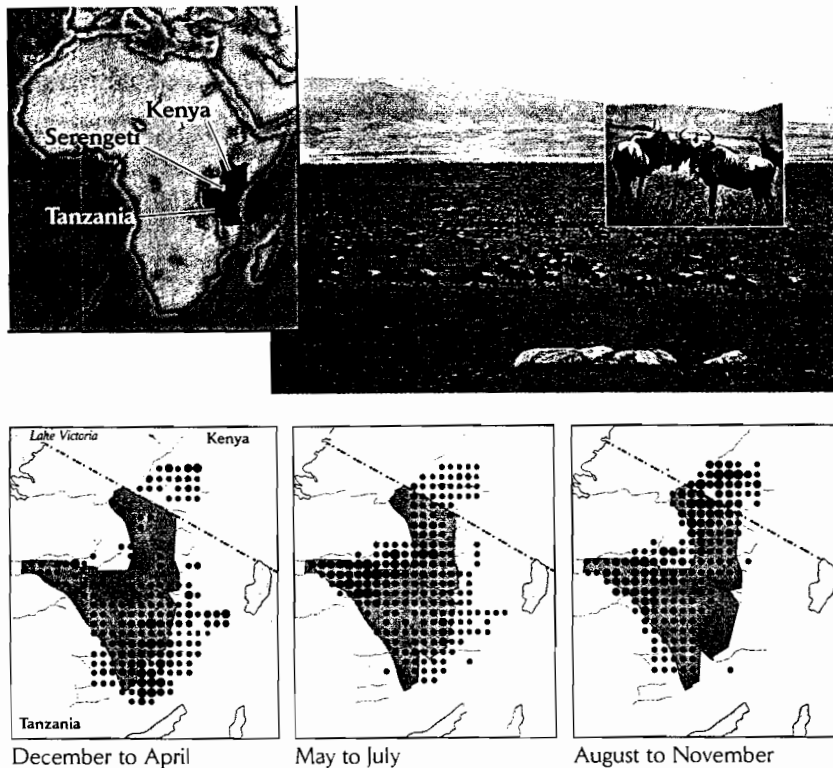
**MORE ON THE WEB** *Rate of phenotypic response.* The mechanisms that organisms use to respond to the environment, as shown by the example of wing-length polymorphism in water striders, must match the pattern of environmental change.



### Migration, storage, and dormancy enable organisms to survive extreme conditions

In many parts of the world, extremes of temperature, drought, darkness, and other adverse conditions are so severe that individuals cannot change enough to maintain their normal activities, or if they could, the change would not be worth the cost. Under such conditions, organisms resort to a number of extreme responses. These responses include **migration**, moving to another region where conditions are more suitable; **storage**, relying on resources accumulated under more favorable conditions; and **dormancy**, becoming inactive.

## Serengeti National Park, Africa



■ **Figure 9.13** The migration of wildebeests follows their food supply. The distribution of wildebeest populations of the Serengeti ecosystem (shaded area) of northern Tanzania and southern Kenya is shown for three times during the annual cycle during 1969–72. The migrations follow lush growth of grasses following seasonal rains in each area. The size of each dot indicates the relative size of the population in that area. Adapted from L. Pennycuik, in A. R. E. Sinclair and M. Norton-Griffiths (eds.), *Serengeti: Dynamics of an Ecosystem*, University of Chicago Press, Chicago (1979), pp. 65–87. Photos courtesy of A. R. E. Sinclair.

## Migration

Many animals, particularly those that fly or swim, undertake extensive migrations. Arctic terns probably hold the record for long-distance migration. Individuals make yearly round trips of 30,000 km between their North Atlantic breeding grounds and Antarctic wintering grounds (where it is the local summer). Each fall hundreds of species of land birds leave temperate and arctic North America, Europe, and Asia for the south in anticipation of cold winter weather and dwindling supplies of their invertebrate food. Populations of monarch butterflies migrate between wintering areas in the southern United States and Mexico to summer breeding areas far to the north into southern Canada. In East Africa, many large ungulates, such as wildebeests, migrate long distances, following the geographic pattern of seasonal rainfall and fresh vegetation (■ Figure 9.13).

Some migratory movements occur in response to occasional failure or depletion of local food supplies, which forces individuals to move out of an area in search of new feeding places. Such movements are perhaps best known from outbreaks of migratory locusts. These migrations occur when locusts leave areas of high local density where food has been depleted. They can reach immense proportions and cause extensive crop damage over wide areas (■ Figure 9.14). Irruptive behavior in locusts is a develop-

mental response to population density. When locusts occur in sparse populations, they become solitary and sedentary as adults. In dense populations, however, frequent contact with other locusts stimulates young individuals to develop gregarious, highly mobile behavior, which can develop into a mass migration.

## Storage

Where environmental changes plunge organisms from feast into famine and migration is not a possibility, storage of resources acquired during periods of abundance for use in times of scarcity may be a way to cope. During infrequent rainy periods, desert cacti swell with water stored in their succulent stems. Plants growing on infertile soils absorb, in times of abundance, more nutrients than they require, and use them when soil nutrients are depleted. In habitats that frequently burn—such as the chaparral of southern California—perennial plants store food reserves in fire-resistant root crowns, which sprout and send up new shoots shortly after a fire has passed (■ Figure 9.15).

Many temperate and arctic animals accumulate fat during mild weather in winter as a reserve of energy for periods when snow and ice make food sources inaccessible. The problem with fat reserves is that heavier animals are often slower and less agile, and therefore are more likely to



■ **Figure 9.14** The migration of locusts is a developmental response to high population density. A dense swarm of migratory locusts moves over Somalia, Africa, in 1962. Courtesy of the U.S. Department of Agriculture.

be caught by predators. One way to avoid this problem is to store food before consuming it. Some winter-active mammals (beavers, squirrels, and pikas) and birds (acorn woodpeckers and jays, for example) cache food supplies underground or under the bark of trees for later retrieval. Often these hoards are immense and may sustain individuals for long periods.



■ **Figure 9.15** Chaparral plants store food reserves in fire-resistant root crowns. In chaparral habitat in southern California, chamise (*Adenostoma fasciculatum*) and other species resprout from root crowns following a fire. These photos were taken September 12, 1979, and April 20, 1980, following a fire near Los Angeles, California. Photos by Tom McHugh/Photo Researchers.

## Dormancy

Environments sometimes become so cold, dry, or nutrient-depleted that animals and plants can no longer function normally. In such circumstances, some species that are not capable of migration enter physiologically dormant states. Many tropical and subtropical trees shed their leaves during seasonal periods of drought; many temperate and arctic trees shed theirs in the fall before the onset of winter frost and long nights. Many mammals, such as ground squirrels, **hibernate** (spend winter in a dormant state) because they cannot find food in winter, not because they are physiologically unable to cope with the harsh physical environment.

In most species, environmental conditions requiring dormancy are anticipated by a series of physiological changes in the individual (for example, production of antifreezes, dehydration, and fat storage) that prepare it for a partial or complete shutdown of activity. Before winter, some insects enter a resting state known as **diapause**, in which water is chemically bound or reduced in quantity to prevent freezing and metabolism drops so low that it is barely detectable. Drought-resistant insects that enter a summer diapause dehydrate themselves and tolerate the desiccated condition of their bodies, or secrete an impermeable outer covering to prevent drying. Plant seeds and spores of bacteria and fungi exhibit similar dormancy mechanisms. Indeed, there are many cases of seeds stored in burial chambers or recovered in other archeological settings that have sprouted after hundreds of years of dormancy. By whatever mechanism it

occurs, dormancy reduces exchange between organisms and their environments, enabling animals and plants to “ride out” unfavorable conditions.

### Stimuli for change

What stimulus indicates to birds wintering in the Tropics that spring is approaching in northern forests? What urges salmon to leave the seas and migrate upstream to their spawning grounds? How do aquatic invertebrates in the Arctic sense that if they delay entering diapause, a quick freeze may catch them unprepared for winter?

In 1938, J. R. Baker made an important distinction between two kinds of cues that trigger these changes. **Proximate factors** are cues, such as day length, by which organisms can assess the state of the environment but that do not directly affect its well-being. **Ultimate factors** are features of the environment, such as food supplies, that bear directly on the well-being of the organism. Virtually all plants and animals sense **photoperiod** (the length of the day) as a proximate factor that indicates season, and many can distinguish periods of lengthening and shortening days. Different populations of a single species may differ strikingly in their responses to photoperiod in different locations, reflecting different relationships of environmental changes to day length. Under controlled cycles of light and dark, southern populations (at 30°N) of side oats grama grass flower in autumn, when day length is 13 hours, whereas more northerly populations (at 47°N) flower in summer, only when the light period exceeds 16 hours each day. In Michigan, at 45°N, populations of small freshwater crustaceans known as water fleas (*Daphnia*) form diapausing broods at photoperiods of 12 hours (mid-September) or less. In Alaska, at 71°N, related species enter diapause when the light period decreases to fewer than 20 hours per day, which happens in mid-August. Warm temperatures and low population densities tend to shorten the day length that triggers diapause (and hence delay the inception of diapause in autumn), suggesting that these factors portend more favorable environmental conditions for *Daphnia*.



### Animals forage in a manner that maximizes their fitness

Because animals live in varied and variable environments, they are constantly forced to make decisions about how to behave. Many of these decisions concern food: where to forage, how long to feed in a certain

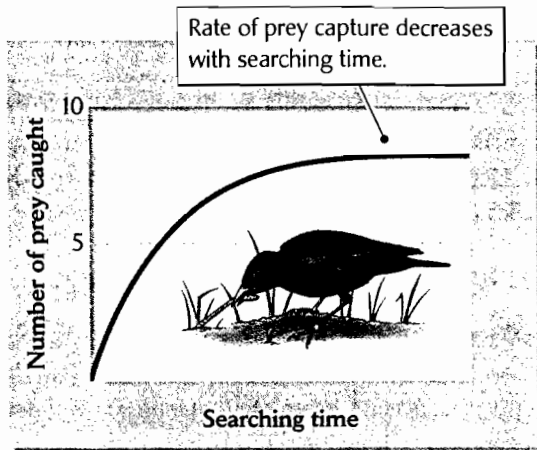
patch of habitat, which types of foods to eat, and so on. Theories of **optimal foraging** seek to explain these decisions in terms of the likely costs and benefits of each possible behavior. Animals are expected to select the behavior that gives the greatest benefit. Cost can be measured in terms of time and energy expended, but the benefit is best judged in terms of evolutionary fitness. However, it is often difficult to measure the consequence of a particular behavioral choice for an individual’s survival and reproductive success. Consequently, ecologists usually measure benefit in terms of factors that are likely to be correlated with fitness, such as amount of food gathered per unit of time. We shall examine a number of behavioral decisions from the standpoint of such costs and benefits. Each of these cases features some aspect of variation in time or space.

### Central place foraging

When birds feed their offspring in a nest, the chicks are tied to a single location, while the parents are free to search for food at a distance. This situation is referred to as **central place foraging**. The greater the foraging range, the greater the amount of food that is potentially available to the parent. But traveling a longer distance also increases the time, energy costs, and risks of travel. Is there some best distance from the nest at which a parent should forage, and how much food should the parent bring to its brood with each trip? That is, how much time should the parent spend gathering food before it returns to its nest?

Studies on the foraging behavior of European starlings allowed investigators to approach these questions from an economic standpoint. During the summer season, starlings typically forage on lawns or pastures for leatherjackets, which are the larvae of tipulid flies (crane flies). Starlings feed by thrusting their bills into the soft turf and spreading the mandibles to expose prey. When they are gathering food for their young, they hold captured leatherjackets at the base of the bill. You can imagine that the more leatherjackets a starling has in its bill, the more difficult it is to capture the next one. For this reason, the time between captures increases as more prey are caught (■ Figure 9.16). That is, as a predator captures more prey, the rate of capture decreases, and the total number of prey increases less steeply. Indeed, a starling cannot continue to feed efficiently with eight leatherjackets in its bill.

Now, from the standpoint of feeding its offspring, the rate at which a parent delivers food to its young is the number of prey caught divided by the length of the for-



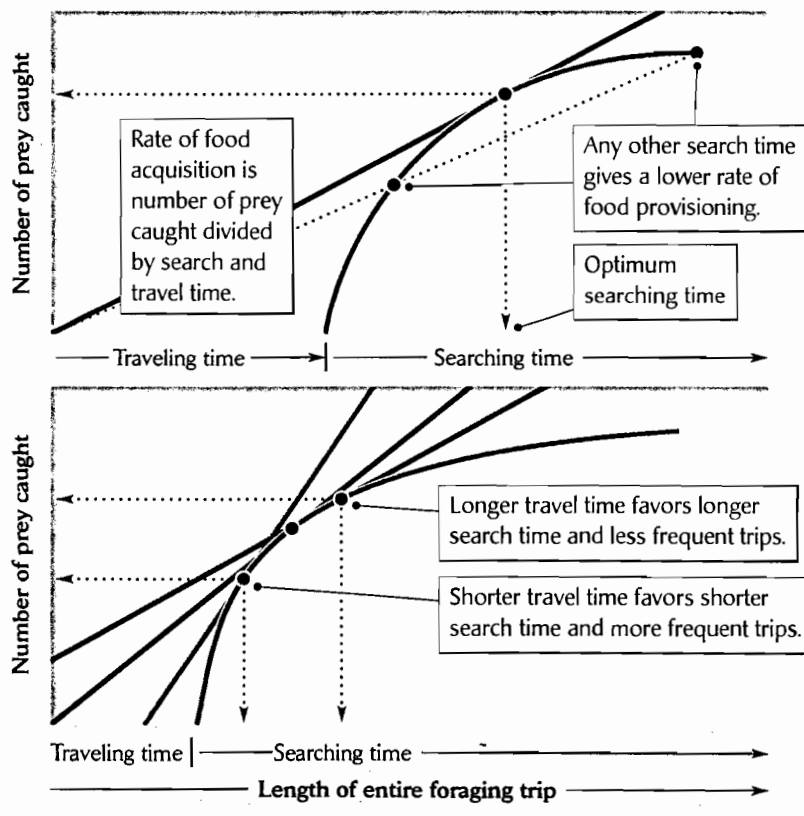
■ **Figure 9.16** Time between captures increases as more prey are caught. The rate of prey captured by starlings declines as foraging (searching) time increases.

aging trip. The foraging trip includes both the time spent at the foraging site and the time spent traveling between the foraging site and the nest. A starling can maximize

the rate at which it delivers food to its chicks by spending an intermediate amount of time in the feeding area during each trip and bringing back something less than the maximum possible amount of food (■ **Figure 9.17**). Imagine yourself in a grocery store where you have to buy as much food as you can in an hour and you have to carry your items by hand. How frequently would you take your items to the cashier? Carrying one item at a time clearly is silly, particularly if there is a long line waiting to be checked out (analogous to a long foraging distance). Trying to carry more than you can handle well, and having to spend time picking up dropped items off the floor and rearranging them, also seem uneconomical. As in the case of the starling with a bill full of leather-jackets, the “law of diminishing returns” sets in. The best strategy is somewhere in the middle. The optimum load varies in direct relation to the traveling time, or more generally, to any fixed cost per trip.

**MORE ON THE WEB**

*Spatially partitioned foraging by oceanic seabirds.* Albatrosses and other seabirds may intersperse long and short foraging trips to gather food alternately for themselves and their chicks.



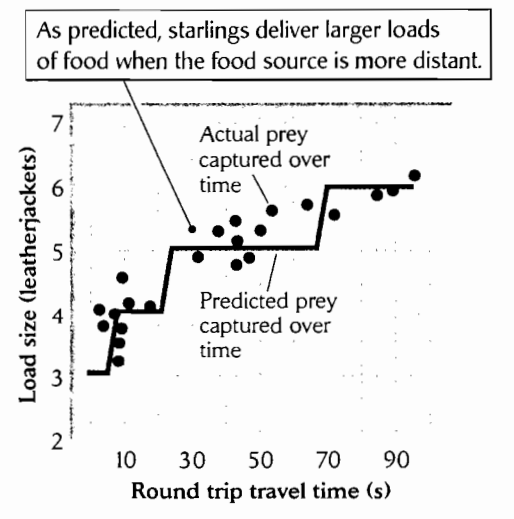
■ **Figure 9.17** Optimal foraging models can be used to predict behavior. For a given prey accumulation curve (orange line), a line passing through the origin of the graph (the beginning of the foraging trip) and tangent to the prey accumulation curve indicates the maximum rate of capture (number of prey caught per unit of time). As shown in the lower graph, the optimal search time on an individual foraging trip increases as the length of the travel time increases.

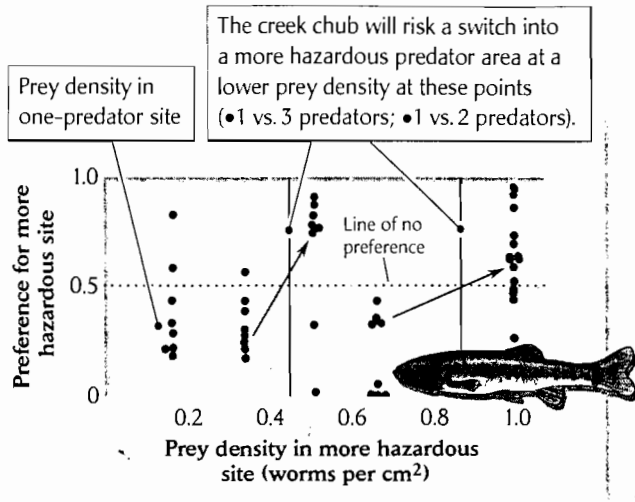
## ECOLOGISTS IN THE FIELD

### Optimal foraging by starlings

To what extent do organisms actually forage optimally? Figure 9.17 is theory. In reality, we have all seen some inefficient shoppers in our local grocery stores. How good are starlings as economists?

This question was addressed in a clever experiment by behavioral ecologist Alex Kacelnik of Oxford University. Instead of letting starlings feed on their natural prey, he trained them to visit feeding tables at which mealworms could be provided through a plastic tube at precisely timed intervals. A starling would arrive at the table, eat the first mealworm, and then wait for the next one to be delivered. Kacelnik adjusted the timing so that each successive mealworm would arrive at a progressively longer interval, mimicking the longer intervals at which a starling would catch leatherjackets as its beak became full. Kacelnik then placed feeding tables at different distances from nests and observed how many mealworms a starling would wait for at different travel times. As expected, starlings increased their load size as travel time increased (■ Figure 9.18). Kacelnik concluded that starlings are good economists, at least when it comes to gathering food.





**Figure 9.19** Foraging fish are risk-sensitive. Chub minnows switch to a more hazardous feeding site only when the prey density in the hazardous site exceeds a certain critical level. The switch point increases with the relative risk of feeding. After J. F. Gilliam and D. F. Fraser, *Ecology* 68:1856–1862 (1987).

poor food item is that it requires time to handle (capture and ingest), during which the forager cannot be looking for other food items. Thus, taking the poorer item may mean that the forager misses an opportunity for a better item. Low-quality food items may also take more time to digest per unit of nutrient or energy obtained, thus reducing an individual’s overall feeding rate.

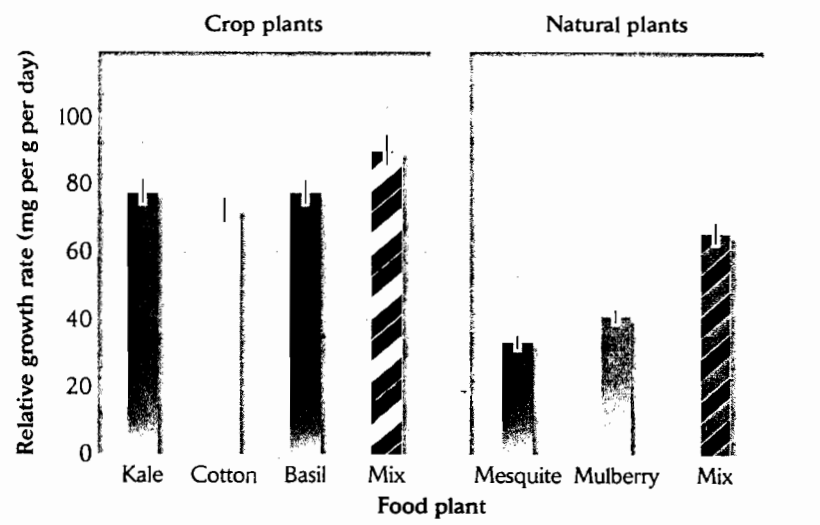
**MORE ON THE WEB** *Optimal prey choice in the great tit.* How poor must an alternative type of prey be for a consumer to pass it up?

### Diet mixing

One reason that some foragers consume a varied diet is that one or a few food items might not provide all necessary nutrients, but these might be present in other food items. Different food types are **complementary** when each contains a required nutrient missing in the other. Humans, for example, can subsist on a diet of rice and beans, but not on either of these alone, because rice and beans each contain essential amino acids missing in the other. The principle of complementarity also applies when foods contain small amounts of different toxins that individually would be dangerous in large doses, but are relatively harmless in the smaller doses ingested with a mixed diet.


The benefits of diet mixing were demonstrated by Elizabeth Bernays and her colleagues at the University of Arizona using nymphs (immature stages) of the grasshopper *Schistocerca americana*. Grasshopper nymphs grew faster when fed a mixture of kale, cotton, and basil than when they were offered any one of these food plants alone (**Figure 9.20**). The effect was even more pronounced on lower-quality, natural food plants, such as mesquite and mulberry: nymphs with mixed diets grew almost twice as fast as those feeding on either one of these plant species alone. Similar results were obtained on artificial diets that were low in either protein or carbohydrates, both of which are required for proper growth. Grasshoppers on mixed diets grew more rapidly than those provided either of the lower-quality foods alone.

Experiments with birds feeding on fruits in the fall in the Morton Arboretum, Chicago, also demonstrated diet mixing. Fruits of two species of shrubs were presented together on artificial “bushes” against a natural background of either one or the other shrub species—that is, with many



**Figure 9.20** Grasshopper nymphs grow faster on mixed diets. Relative growth rates of *Schistocerca* grasshopper nymphs fed mixed diets exceeded growth rates on uniform diets, whether comparisons were made with crop plants or natural food plants. After E. A. Bernays et al., *Ecology* 75:1997–2006 (1994).

shrubs of the background species in the immediate vicinity—and fruit consumption was then recorded. The results support the hypothesis of complementarity in that birds selected the fruit that contrasted with the background fruit supply. For example, rough-leaved dogwood (*Cornus drummondii*) and pokeweed (*Phytolacca americana*) are similarly sized (7.4 and 8.9 mm) fruits with high lipid/low sugar and low lipid/high sugar contents, respectively. In a paired choice test, in an area with abundant natural dogwood, 3.2% of dogwood and 29% of pokeweed fruits were consumed; in an area with abundant natural pokeweed, 97% of dogwood and 71% of pokeweed fruits were consumed. In other words, the birds showed a preference for the less abundant alternative.



## Summary

1. Most of the traits of organisms have evolved in response to their environments, including variation in environmental conditions and resources. For this reason, an understanding of evolution is essential to interpreting adaptations to varying environments.

2. Evolution by natural selection occurs when genetic factors influence survival and reproductive success. The genetic characteristics of those individuals that achieve the highest reproductive success increase in the population with time.

3. The genotype includes all the genetic factors that determine the structure and functioning (which together constitute the phenotype) of an individual. Many genetic factors have unique, measurable effects on the phenotype.

4. Individual organisms can respond to changes in their environments by altering their behavior, physiology, or morphology. Such changes are referred to as phenotypic plasticity.

5. Organisms have characteristic activity spaces defined by the conditions within which they can live and reproduce.

6. The availability of suitable activity space for an individual depends on the range of conditions and resources in the environment at any given time.

7. Animals select microhabitats whose physical conditions fall within their activity space.

8. Acclimation involves reversible changes in structure (for example, fur thickness) or biochemical pathways (changes in the amounts of different enzymes). Such changes require longer periods (usually days or weeks) than behavioral or

metabolic changes. Acclimation plays a prominent role in responses of long-lived organisms to seasonal change.

9. Developmental responses express the interaction between an organism and its environment during its growth. Different environmental conditions lead to different characteristic, irreversible structures and appearances.

10. When conditions exceed the range of tolerance, organisms may migrate elsewhere, rely on materials stored during periods of abundance, or enter inactive states.

11. In many cases, the individual must anticipate environmental changes in order to respond successfully. Organisms rely on proximate cues, such as day length, to predict changes in ultimate factors, such as food supply, that directly affect their well-being.

12. Food supplies vary spatially, temporally, and with respect to the quality of prey items. Thus, animals must make choices about when, where, and how to feed that maximize their reproductive success.

13. Central place foragers, which must deliver food to a fixed place, such as a nest with young, balance the costs and risks of travel against the size of the area within which they can forage.

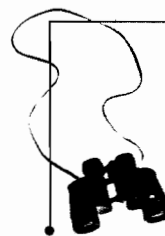
14. The quality of a feeding area is affected by the risk of predation on a foraging individual. Many animals avoid feeding in high-risk areas even though food may be plentiful. This strategy is referred to as risk-sensitive foraging.

15. Some foragers consume a mixed diet to obtain an appropriate balance of required nutrients or to reduce levels of toxic substances in their diets. Diet mixing is especially common among animals that feed on plants.

## PRACTICING ECOLOGY

### CHECK YOUR KNOWLEDGE

#### *Tolerance of Variable Environments*



We started this chapter by discussing how organisms cope with climate variability in the Mojave Desert. Indeed, this desert is hot in the summer. But it also can be cold in the winter, when air temperatures regularly fall below 0°C. Thermal extremes, which can limit the distributions of plants and animals, often occur in brief episodes, such as heat waves and cold snaps, and are not so apparent in annual averages. However, this kind of short-term variability can severely decrease the capacity of organisms to survive and reproduce. Consequently, extreme conditions help explain the

geographic distributions of many species. For example, the northern limit of the creosote bush *Larrea tridentata* matches the southern extent of minimum temperatures down to  $-18^{\circ}\text{C}$  in the Mojave Desert. Creosote bush, particularly seedlings, cannot tolerate colder winter temperatures.

Besides accommodating temperature extremes, plants will have to adapt to variations in the environment caused by increasing atmospheric carbon dioxide. Burning fossil fuels and cutting forests will alter the global climate, perhaps substantially. The resulting increases in air and soil temperatures and changes in soil water and nutrient content are expected to have dramatic implications for the productivity and distribution of terrestrial vegetation in both natural and managed ecosystems. For example, as winter temperatures increase, the distributions of plants such as creosote bush will likely shift northward and to higher elevations. Plants also respond directly to elevated  $\text{CO}_2$ . Elevated atmospheric  $\text{CO}_2$  increases photosynthetic efficiency, but this effect often decreases upon long-term exposure. In certain ecosystems, exposure to elevated  $\text{CO}_2$  can also cause a reduction in leaf water loss. Plants in arid lands, such as the Mojave Desert, may benefit from this water saving more than those in other biomes.

Recent studies by Stan Smith, James Coleman, Robert Nowak, and Jeffrey Seemann at the Nevada Desert FACE Facility have focused on the ability of plants to tolerate stressful conditions. "FACE" is an acronym for "Free Air Carbon Enrichment," a procedure in which large quantities of carbon dioxide gas are released directly to the atmosphere at ground level over small areas. Thus plants can be exposed to elevated  $\text{CO}_2$  in natural environments. This method avoids complicating factors caused by exposing plants inside greenhouses, which alter the climate in unrealistic ways. One of the studies from this project has compared the ability of *Yucca brevifolia* (the Joshua Tree), *Yucca schidigera* (the Mojave Yucca), and *Yucca whipplei* to withstand high-temperature extremes under predicted  $\text{CO}_2$  concentrations of the future. In this and other studies, elevated  $\text{CO}_2$  has been shown to have a direct impact on the responses of plants to environmental variability.

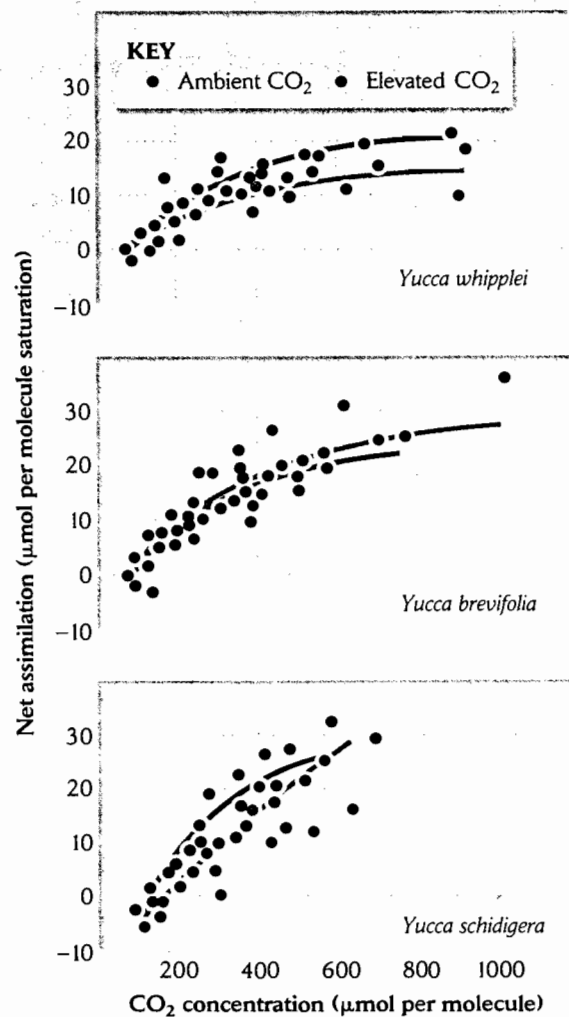
#### CHECK YOUR KNOWLEDGE

1. Why is it important to understand the responses of desert organisms to their physical environment?
2. Refer to ■ Figure 9.21. Which of the *Yucca* species exhibits the greatest effect due to elevated  $\text{CO}_2$ ? What is the effect of elevated  $\text{CO}_2$  on the magnitude of photosynthesis?
3. How do the three different *Yucca* species vary in their responses to elevated  $\text{CO}_2$  and high-temperature events?

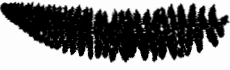
From this, what general conclusions can you draw about the results of global change experiments?

**MORE ON THE WEB**

4. Go to the Weather page of the Nevada Desert FACE Facility from *Practicing Ecology on the Web* at <http://www.whfreeman.com/ricklefs> and examine the temperature and precipitation records measured at this site. By how much do they vary from summer to winter? And from year to year? What does this require of plants and animals in terms of evolution of adaptations to climatic variability?



■ **Figure 9.21** Curves for three species of *Yucca* exposed to either ambient or elevated  $\text{CO}_2$  in a glasshouse, prior to the temperature increase. Red symbols and lines are from ambient plants, while blue symbols dotted lines are from elevated plants. From T. E. Huxman, et al., *Plant, Cell and Environment* 21:1275–1283.

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