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Dispersal may involve the movement of single individual or large groups such as these elephants.

11

Dispersal

Populations are not static. That is, their members and gametes are not restricted to staying within the boundaries of the population. Individuals may move to seek a different place to feed or to overwinter. This type of migration is typical for many birds that live in temperate climates. Bird migrations may cover thousands of miles. These movements let birds avoid harsh winter conditions and find new sources of food. Other organisms may travel that far, but not under their own power. Many marine organisms travel thousands of miles while floating on the ocean currents.

These movements can have both ecological and genetic consequences. Dispersing individuals may find new suitable but unoccupied habitats and thereby initiate new robust populations. Even small numbers of new emigrants may carry genetic variation that is not currently in the population. These individuals can have a large effect on population differentiation.

Many organisms have no effective means of movement. These organisms can choose an alternative strategy of dormancy. Either the adults or some juvenile form may simply assume a more robust condition and try to weather out the bad conditions. Plants obviously lack the ability to move, and they exhibit many types of dormancy—especially with seeds. In this chapter we will develop these ideas so that the full ecological, genetic, and evolutionary significance of dispersal, migration, and dormancy can be well understood. ❖

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DISPERSAL AND MIGRATION

11.1 Migration and dispersal have a variety of important genetic and ecological consequences

Animals and plants have a wide variety of ways to move from one place to another. Dispersal may be passive or active. In **passive dispersal**, whole organisms, their gametes, or their seed are carried by currents of air and water or attached to moving animals. Passive dispersal is not necessarily haphazard dispersal. Organisms that depend on passive disperal often have elaborate structures to take advantage of wind or air currents. Seeds, for example, may have structures resembling sails or propellers that allow them to travel farther in gusts of wind (Figure 11.1A). We will see in this section that the physical environment can profoundly influence the distribution of animals that rely on ocean currents to disperse their larvae.

In **active dispersal**, organisms, especially animals, disperse under their own power and so may control the distance and direction that they travel. This dispersal can be very dramatic and regular with animals moving in large cohesive groups between two locations. Such dispersal is called **migration**. Bird migration may cover distances of 10,000 miles or more. Migrations are often seasonal, but they may be more frequent. For instance, animals following the tides may move several times a day, as the height of the tide changes.

Less organized dispersal includes individuals moving away from a local population or group. Individuals settled in a particular area may still move substantial distances within some characteristic area or **home range** just to find food or a mate. Later in this section we will explore the relationship between the size of the home range and the energy requirements of a particular animal.

Migration between Populations Links Their Fates

Population size may vary, due either to the imperfect action of density-dependence or to changes in the environment. Occasionally these population fluctuations may become severe enough that a population goes extinct. Yet these periods of population extinction may be brief if populations frequently exchange migrants with nearby populations, since migrants may recolonize an extinct population. For this reason, predicting the long-term fate of a population depends not only on the characteristics of the individual population but also on other populations that may communicate with it via the process of migration.

Genetic Polymorphisms for Dispersal

In some organisms the propensity to disperse is under genetic control. Such systems are interesting because they allow us to analyze the consequences of dispersing. For example, to assess the fitness consequences of dispersing, we can keep track of the survival of those individuals in a specific environment that do not disperse versus those that do disperse. If environmental conditions occasionally deteriorate, due either to crowding or to seasonal fluctuations in resources, the ability to disperse can increase an organism's chances of finding a new, suitable environment. The frequency of dispersing forms in many species appears to be highest in the environments that are subject to these types of deterioration.

FIGURE 11.1A Some plants produce seeds that are designed to take advantage of wind dispersal.

So why, for example, don't all insects disperse? The energy needed to form wings and wing muscle may actually detract from an individual's ability to produce offspring. It may not always pay to invest in the machinery needed to disperse. This uncertainty in the relative benefits of dispersing or staying put is reflected in some species where only a part of the population has the capability to disperse. In these cases, we say the population is **polymorphic** for dispersal ability.

Two species of *Gryllus*—*G. firmus* and *G. rubens*—have a genetically based wing polymorphism. The wingless form (bottom in Figure 11.1B) does not disperse; and it has less wing muscle, lower

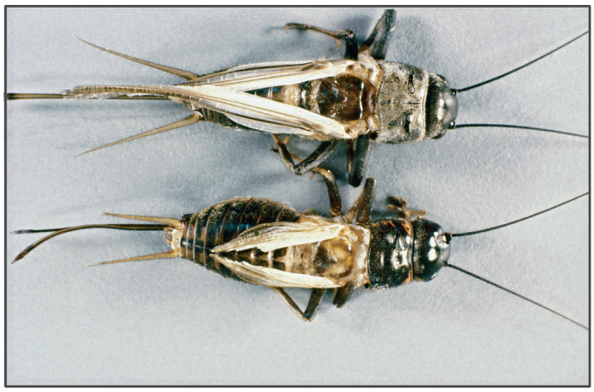

FIGURE 11.1B The Two Winged Morphs of the Cricket *Gryllus*
On the bottom is the wingless form; on the top is the winged morph.

metabolic rate, and greater ovary weight than the winged form (top, Figure 11.1B). Males of the wingless form have higher mating success. The price for dispersing is reduced fertility in both males and females.

Whether a given individual develops wings or not is determined by an insect hormone called *juvenile hormone*. During the last larval stage, the wingless forms have higher levels of juvenile hormone than do the winged, and this prevents the development of wings and wing muscle. The amount of juvenile hormone in an insect is, in turn, finely controlled by levels of juvenile hormone esterase, an enzyme that breaks down juvenile hormone.

Tony Zera and his colleagues have shown that the levels of juvenile hormone esterase can easily be raised or decreased by artificial selection. This observation tells us not only that the level of juvenile hormone esterase in an insect is under genetic control, but that there is genetic variability in populations for this genetic control. Thus, we would expect that natural selection can control the frequency of dispersal by changing juvenile hormone esterase levels.

11.2 A population may consist of many small populations linked by migration

So far we have treated populations as isolated groups of individuals. In fact, many species consist of a large number of populations that are linked through occasional exchange of migrants. This collection of groups is sometimes called a **metapopulation**. What happens to the whole metapopulation may differ from what happens to its constituent groups.

We have already seen how density dependence affects population size (Chapter 10). Density dependence and environmental fluctuations may cause populations to go extinct. Populations may also fluctuate for other reasons, such as the impact of predators. Without migration, those habitats where extinction has occurred would remain unoccupied. But migration can reintroduce a species and thus prevent the progressive extinction of all populations. Figure 11.2A describes an experiment that shows the differing fates of large single populations and metapopulations.

Migration can be both stabilizing and destabilizing. Figure 11.2B shows a hypothetical metapopulation consisting of 10 smaller populations. Each of these has some chance of going extinct in a particular period of time. If there were no migration between these populations, then all 10 populations would eventually become extinct. But if migration occurs at a rate (m) that exceeds the rate of extinction (e), then the metapopulation will approach an equilibrium. What happens if the migration rate gets too large? Then the equilibrium will not be stable, just as the carrying capacity is not stable if r, the intrinsic rate of increase, becomes too large. ❖

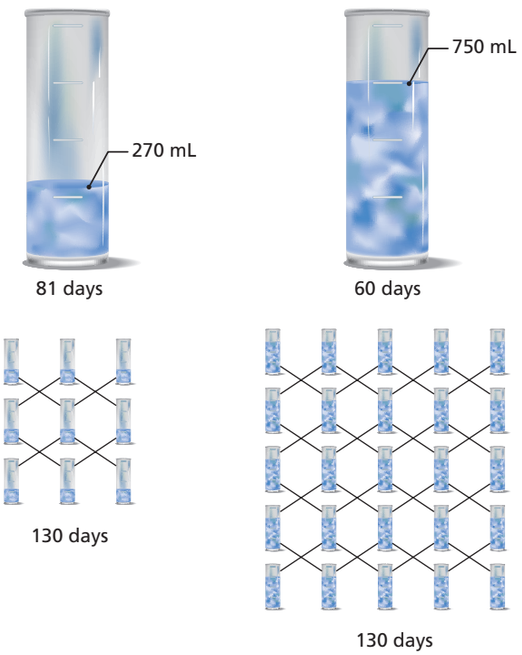

FIGURE 11.2A Holyoak and Lawler (1996) created laboratory populations of single-celled ciliates. The prey species was *Colpidium stritum*, which was eaten by the predator ciliate, *Didinium nasutum*. The predator and prey were kept in two types of environments: (1) a large single culture, which was either 270 mL or 750 mL in volume; and (2) a metapopulation. The metapopulation consisted of either 9 (30 mL) small bottles joined by hollow tubes or 25 (30 mL) bottles joined by hollow tubes. The numbers of predator and prey were determined at regular intervals. The average time until all predators went extinct was calculated from this information. In the metapopulations, the predators persisted until the end of the experiment (130 days). In the large single populations, the predators went extinct well before the end (81 days for the 270-mL culture and 60 days for the 750-mL culture).

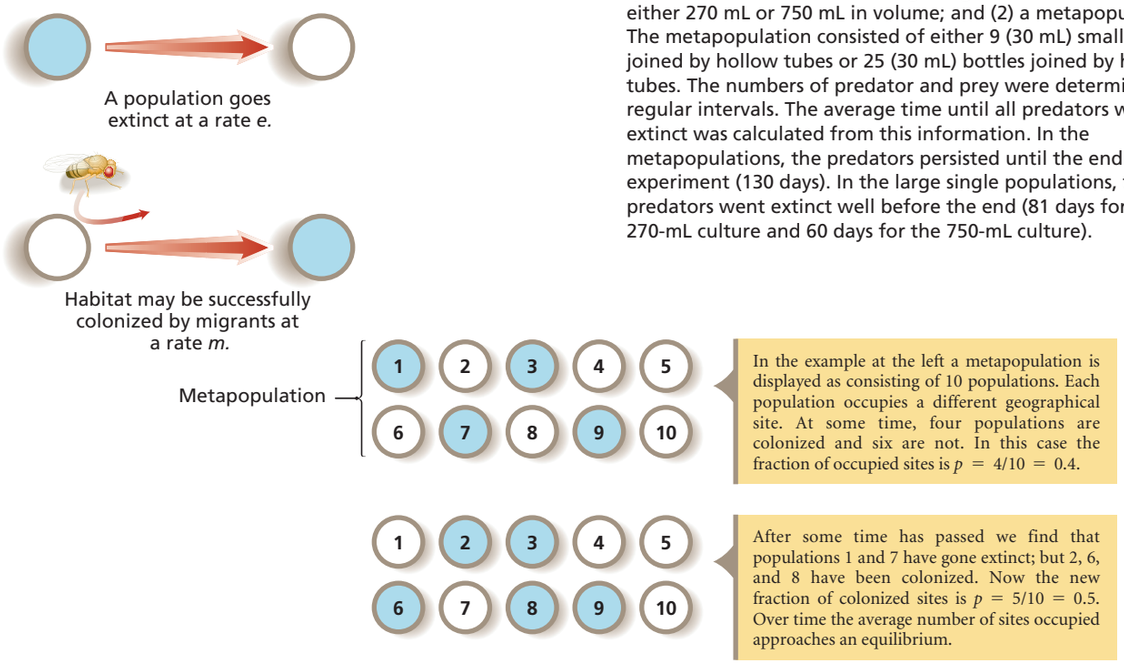

FIGURE 11.2B In a metapopulation, individual populations may go extinct, and unoccupied habitats may be colonized by migration. If the rate of migration is greater than the rate of extinction, the fraction of colonized sites will approach an equilibrium value of 1– (e/m). As shown here, however, the precise sites that are empty and occupied will always be changing.

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Home-range size is related to energetic requirements 11.3

In the search for food, shelter, or mates, many animals move within characteristic areas called home ranges. The movement that determines the home range is more limited than that of dispersal. An individuals' home range may also change over time, especially when seasons affect the availability of food.

While it is usually not difficult to monitor the movements of animals in their home ranges, it is not always obvious why individual animals move. But sometimes we can explain particular patterns of movement. For instance, in species where males mate with multiple females, males often move more widely than females, because they are searching for *both* food and mates.

What factors affect the size of the home range? There are several:

1. *Diet of the animal* Carnivores have to search greater distances than herbivores do, all other things being equal, because their prey is mobile and sparse compared to plants. Part (i) in Figure 11.3A shows these trends in data from carnivores and herbivores.
2. *Size of the organism* All other things being equal, larger animals need more energy than smaller animals do, so they need to search over greater distances to get the required food. Part (ii) in Figure 11.3A shows for both birds and rodents that larger animals require more energy.
3. *Distribution of food resources* If the food is patchy in its distribution, then animals may have to travel greater distances to find sufficient food.

The relationship between home-range size and energetics can usually be described by a simple mathematical relationship. In the following equation, W is the weight of the organism, a is a constant reflecting the organism's basal metabolism, and b is a constant indicating the rate at which energy requirements increase with size:

$$\text{Energy} = aW^b$$

Animals that require more energy will have larger home ranges; see part (iii) in Figure 11.3A. For example, in both birds and rodents, the constant b is roughly the same, while the constant measuring basal metabolism, a, is greater for birds than for rodents. The higher basal rate for birds reflects the high energy costs of flight.

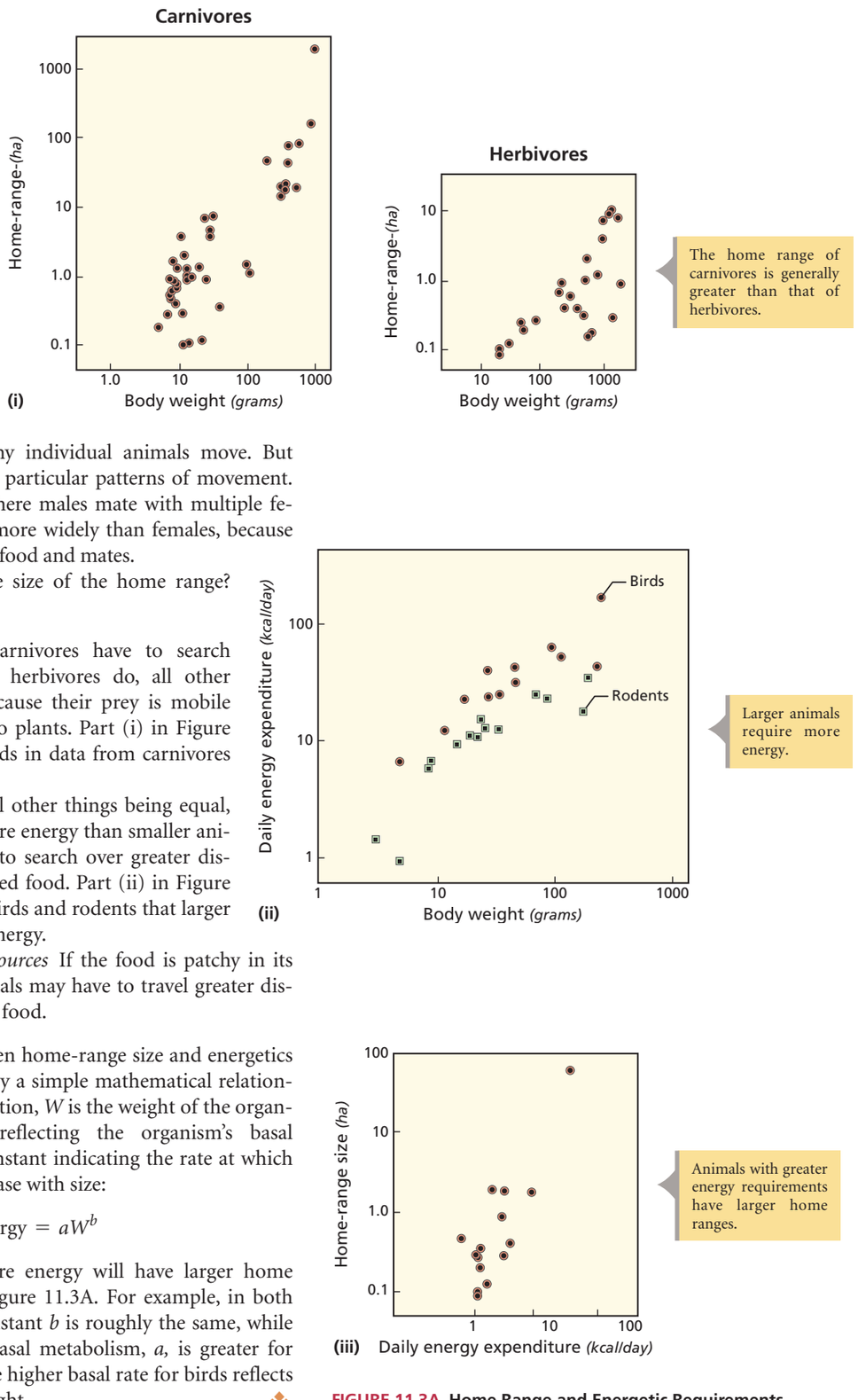

FIGURE 11.3A Home Range and Energetic Requirements

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11.4 The dispersal of many marine organisms is mediated by ocean currents

We have seen the importance of space as a limiting resource in the intertidal environment (Module 10.4). Ocean currents play a crucial role in dispersing juvenile forms of many plants and animals that live in the intertidal zone. These physical factors also contribute to the relative differences in free space along the West Coast of the United States (see Figure 10.4D). These important biological consequences of ocean currents warrant a closer examination of the forces causing ocean currents.

As an example, let's look at the local movement of water off the West Coast of the United States, the area that is home to the barnacles and sea anemones we discussed in Chapter 10. One important force contributing to currents in this area is the **Coriolis effect**, which arises from the Earth's rotation. Viewed from the North Pole, the Earth rotates in a counterclockwise direction. Because of the Earth's rotation, drifting objects appear to deviate from a straight line.

Figure 11.4A shows one way to envision this phenomenon. Imagine you are on a carousel that is moving in a counterclockwise direction (observer X in Figure 11.4A). If an individual in the center of the carousel throws a ball to someone standing directly behind you (observer B in the figure), the ball will appear to veer off to the right. The Coriolis effect is more complicated than this, because the Earth is a rotating sphere instead of a circular carousel. Viewed from the South Pole, it rotates clockwise, so the ball would appear to veer to the left; nevertheless, the general principle holds true.

During the summer months, a strong and fairly consistent north-south wind develops off the west coast of North America. The force of the wind on the surface waters, along with the Coriolis effect, produces a westward, offshore flow of water (Figure 11.4B) called an **Ekman flow**. As the surface water moves off to the west, it is replaced by deep, cold water that moves up to the surface. This flow of cold water to the surface is called **upwelling**. Upwelling is responsible for the very cold summer water temperatures along the west coast. The upwelled water often has higher levels of phosphorus due to the organic matter brought up from the ocean bottom. This phosphorus can support additional growth of **phytoplankton**, the microscopic plants that grow in the ocean waters.

How does the Ekman flow affect the dispersal of intertidal larvae? Figure 11.4C illustrates two ways. First, young larvae are carried away from the shore and out to the ocean by this flow. The maximum distance that intertidal larvae travel away from the shore is proportional to the strength of upwelling, as Figure 11.4C (left graph) shows. (In Figure 11.4C, a positive upwelling index indicates that the current is moving offshore, while a negative index means the water is actually flowing onshore). Second, the Ekman flow will also make it more difficult for larvae to make it back to the shore when they are mature, so the settlement of larvae on the central California coast decreases as the strength of upwelling increases, as Figure 11.4C (right graph) shows.

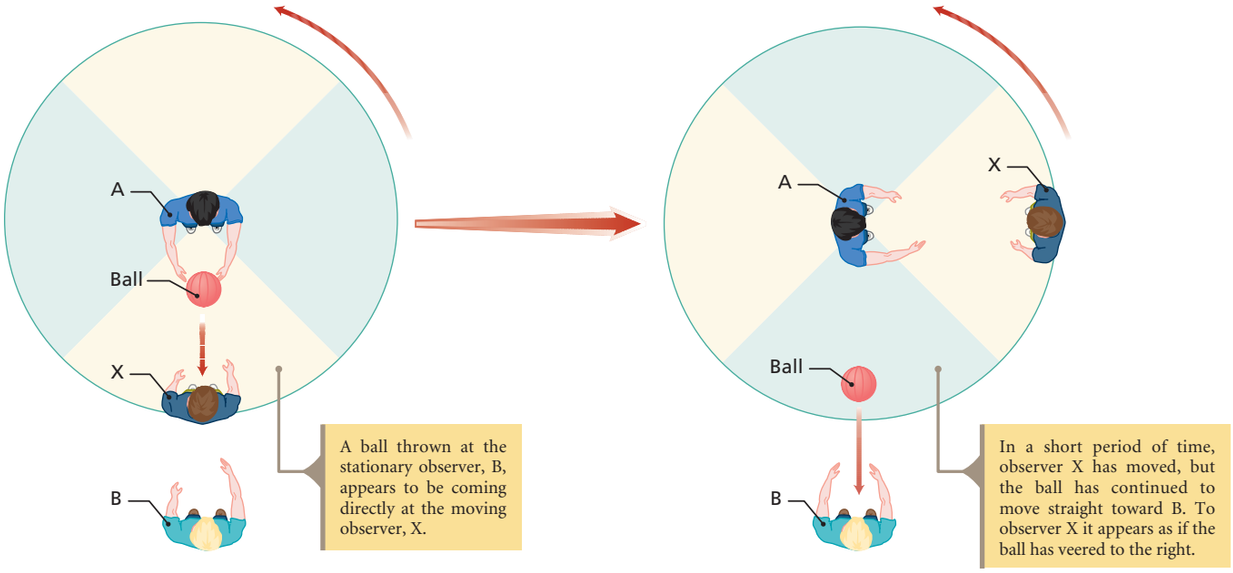

FIGURE 11.4A **The Coriolis Effect**

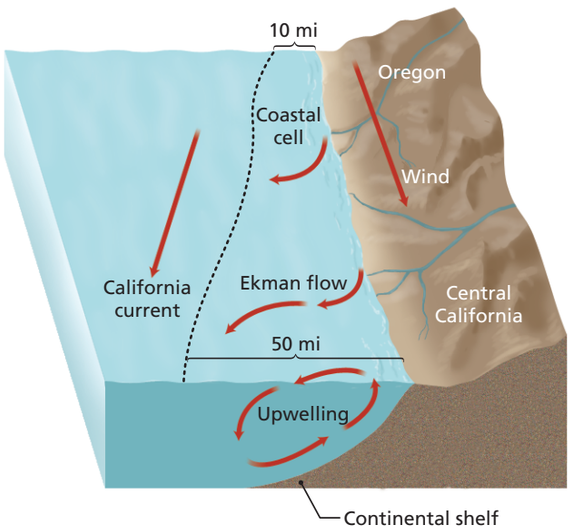

FIGURE 11.4B **Upwelling** Winds moving from north to south along the West Coast of the United States create an Ekman flow of surface water away from the coast. This surface water is replaced by cold water deep below the surface.

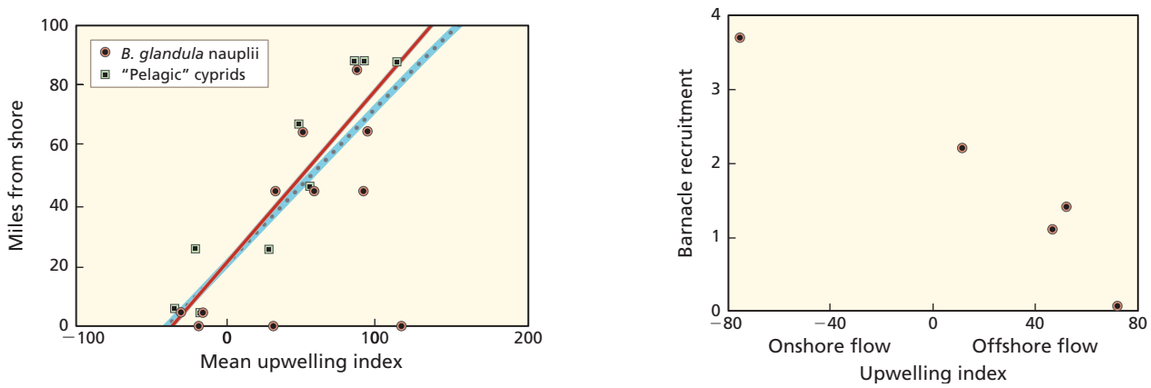

FIGURE 11.4C The figure at left shows the distance larvae are transported as a function of the strength of upwelling (upwelling index). The figure at right shows that barnacle recruitment onshore depends decisively on the direction of currents and their strength (after Roughgarden et al., 1988).

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11.5 Plant morphology affects the efficiency of passive dispersal

How do plants disperse? Because plants are not mobile, seeds and spores are responsible for the dispersal of plant populations. Pollen also leads to gene flow between populations.

Dispersal of seeds, spores, and pollen often depends on help from environmental factors or other organisms. Many seeds are dispersed by the wind, and they may even have special structures that help accomplish this purpose. Animals are frequently critical partners in dispersal of seeds, spores, and pollen. For example, when an animal eats a fruit, the seed in the fruit passes through the animal's digestive tract undigested and is later deposited in the feces, often quite far from the original plant. Other seeds become attached to the fur, bristles, skin, or feathers of animals, which transport the seeds as they move.

Animals are frequently critical partners in dispersal of both seeds and pollen.

Animals are also instrumental in dispersing pollen of many plants. An interesting example involves the plant *Ipomopsis aggregata* (Figure 11.5A). Individual plants of this species produce both male (pollen) and female (seeds) gametes. However, individual plants cannot fertilize their own seeds, so they must **outcross**, using pollen from another individual. These plants are most often pollinated by hummingbirds (Figure 11.5B). Diane Campbell and her colleagues (1996) have carefully documented the dispersal of pollen from individual plants by marking pollen with fluorescent dye and then following the marked pollen to other plants. The biologists found that the amount of pollen exported during each hummingbird visit is proportional to the size of the flower's corolla, for two reasons. (1) Flowers with wider corollas also produced more total pollen. (2) The amount of pollen removed by an individual bird was greater for flowers with larger corollas than for flowers with smaller corollas. Pollen transfer by plants with wide corollas seems to be more efficient. Hummingbirds inserted their bills deeper into flowers with wide corollas and thereby extracted a greater amount of pollen (Figure 11.5B).

FIGURE 11.5A ***Ipomopsis aggregata***

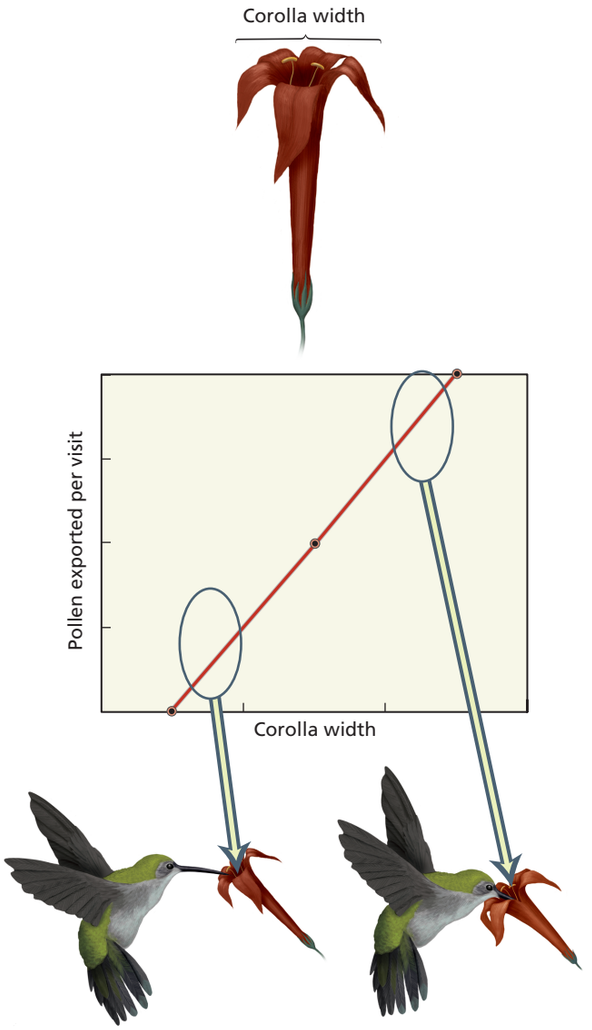

FIGURE 11.5B Hummingbirds place their bills deeper in flowers when the corollas are wide. The deeper the bill, the more pollen is transported.

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Some species escape bad conditions by "traveling" through time: dormancy 11.6

Dispersal is an adaptation that takes plants and animals from an inhospitable environment to an environment in which survival or reproduction are more likely. But many plants and animals cannot effectively disperse (Figure 11.6A.) Some species cannot disperse because they and their gametes are not significantly motile. This is evidently true of many plants, which obviously lack locomotion and may also lack dispersing pollen or seeds. This is also true of sessile animals, such as sponges and sea anemones. Fissile sea anemones even lack a dispersing life-cycle stage, unlike barnacles, which disperse widely as juveniles before becoming sessile as adults.

Organisms that do not disperse are at the mercy of local conditions. Unfortunately, such local conditions may become inimical to the continued survival or reproduction of the organism. Physical trauma may injure sessile forms. Extremes of temperature, light, moisture, and desiccation may kill or damage the organism. Overcrowding may limit the resources available to an organism, impairing its survival or reproduction. But without dispersal, what can be done?

One solution is dormancy. Dormancy is an adaptation that involves shutting down most metabolism, enabling the organism to survive on little or no food. Dormancy also reduces vulnerability to external stressors, possibly including heat and desiccation. The Darwinian opportunity is that the period of dormancy could be followed by a more active period during which survival and reproduction are feasible. Dormancy becomes a way of "traveling" through time to a better habitat. Dormancy can be an effective alternative to dispersal.

Perhaps the most familiar example of dormancy is the hibernation of bears from temperate climates (Figure 11.6B). The reduction in metabolism enables bears to survive most of the winter, with little foraging or feeding. Other forms of dormancy can be much more radical. Plant seeds, in some cases, are almost completely shut down metabolically.

FIGURE 11.6A Plants and Animals with Limited Dispersal Ability: (i) strawberries and (ii) fissile sea anemones

Rather than a single simple adaptation, dormancy is exhibited over a diverse range of species, with widely varying consequences for the ecology and evolution of those species. For some species, dormancy is brief. For other species, dormancy is part of a seasonal life cycle. For still other species, dormancy may allow the species to travel many years through time, with more impact on population genetics than on dispersal. This temporal range is shown in Figure 11.6C.

FIGURE 11.6B Grizzly Bear Pulls Leaves into its Den

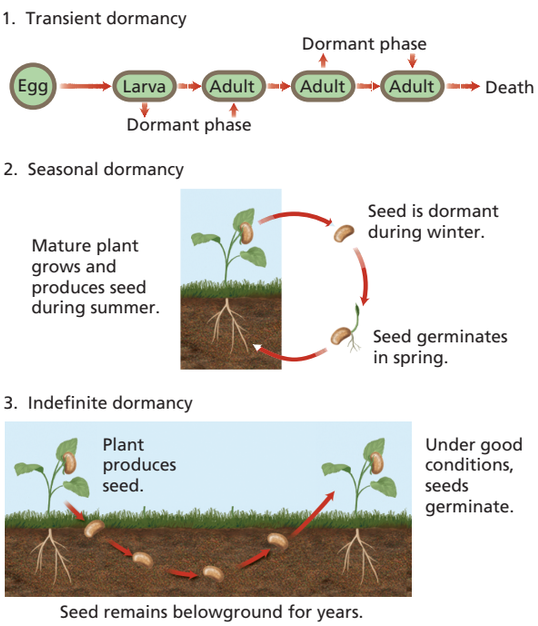

FIGURE 11.6C Patterns of Dormancy

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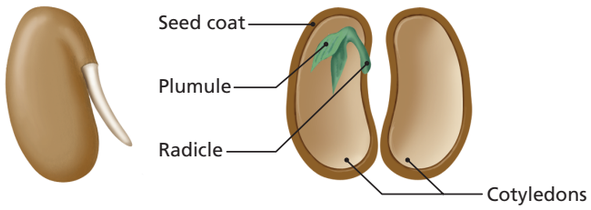
11.7 Plant seeds are some of the longest-lasting dormant life-cycle stages

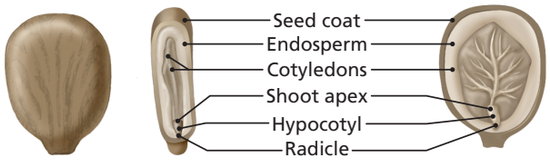
After fertilization, seeds store nutrients and reduce their water content. A *seed coat* covers the surface of the seed, and the coat is thick and hard in a number of species. The coconut shell is a famous example of the physical robustness attained by some seed coats. (Figure 11.7A shows several seed structures.) In many respects, seeds are among the most invulnerable of all forms of life, resisting heat, freezing, desiccation, water, and so on.

Once the seed has fully developed, it enters into a period of dormancy in which its metabolic rate is extremely low. Growth and development entirely cease. The seed is perhaps the most perfect resting stage exhibited by multicellular life. Plants distribute seeds widely. The soil of many habitats contains a hidden reserve of dormant seeds called a **seed bank**. Seed banks link generations through time: seeds produced decades earlier may lie dormant in soil, although the seeds of many species are viable for just a few years (see Figure 11.7B). Dormancy may thereby connect otherwise isolated biological generations, increasing the breeding population size and reducing genetic drift.

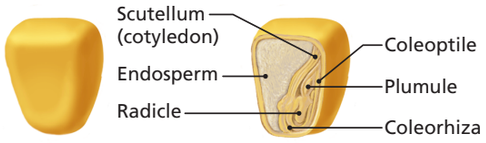
The adaptive significance of the seed is that it allows a plant to disperse dormant offspring through space and time until changed conditions allow *germination*, when the developing plant, or *seedling*, is produced by the seed. The timing of germination is crucial. A very interesting feature of plant biology is the environmental cues that seeds use to trigger germination. Benign conditions for seedling growth often serve as cues, especially reasonable moisture. Because seeds are quite dry, they naturally tend to take up water. This can



1. Common bean. The fleshy cotyledons of the common garden bean, a dicot, store food that was absorbed from the endosperm when the seed developed.



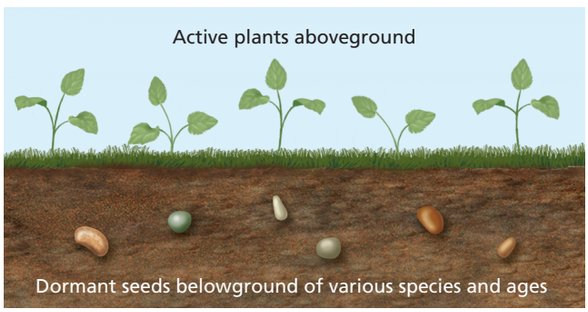
2. Castor bean. The castor bean has membranous cotyledons that will absorb food from the endosperm when the seed germinates.



3. Corn. Like other monocots, corn has only one cotyledon (the scutellum.) The rudimentary shoot is sheathed in a structure called the coleoptile.

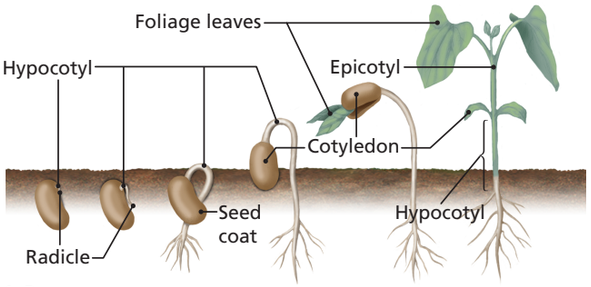
FIGURE 11.7A Seed Structure

lead to the rupturing of the seed coat, with germination following straightforwardly. Germination occurring in different plants is shown in Figure 11.7C, proceeding to the right. Germination can also be triggered by quite different cues—including fire, an important ecological agent in some habitats, such as the California chaparral where many grasses and shrubs germinate in response to fire.

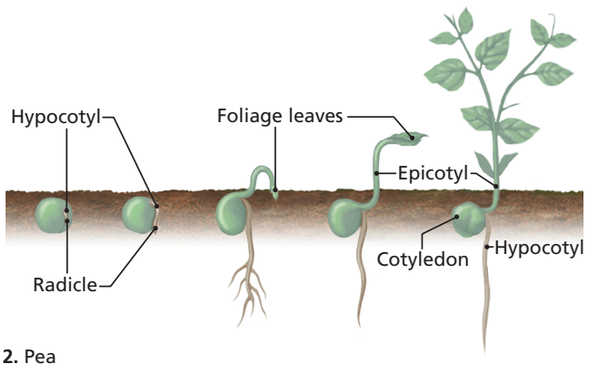


Seeds may germinate whenever conditions are good, as long as they are still viable.

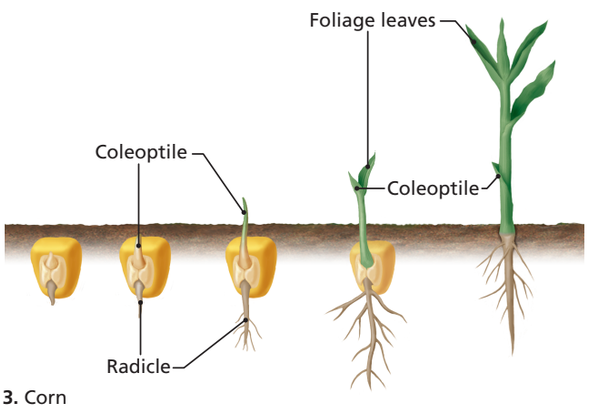
FIGURE 11.7B A Seed Bank



1. Bean

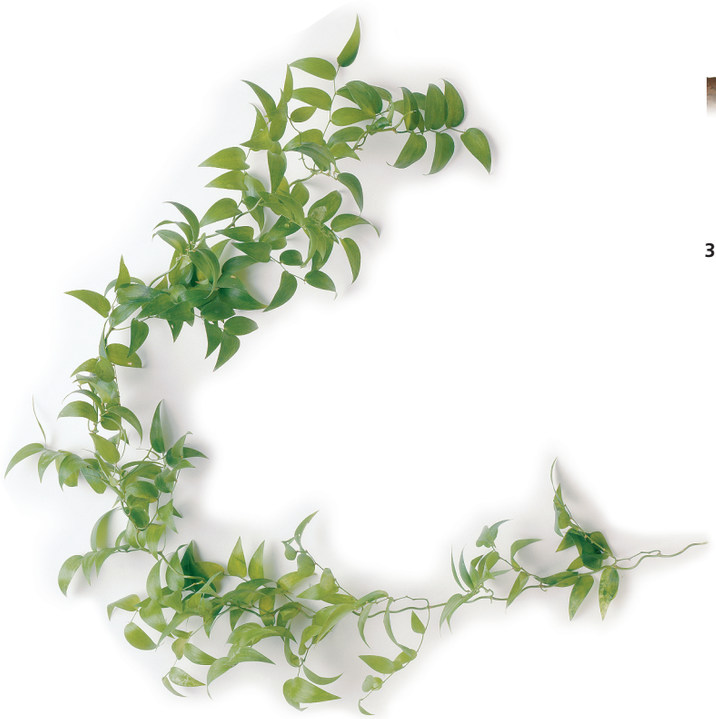


2. Pea



3. Corn

FIGURE 11.7C Seed Germination



11.8 Many animals and plants survive in seasonal climates through the use of dormancy

Although equatorial ecosystems have relatively stable environments, toward the poles all habitats are affected by extreme annual fluctuations in temperature. Indeed, the circumpolar environment may entirely forestall completion of the life cycles of most invertebrates, and most plants, for most of the year.

The solution that many species have found is to spend much of the year in a dormant phase. In plants, the primary form of seasonal dormancy is the seed stage. Because of their low water content, seeds are particularly resistant to the formation of ice crystals, the main agent of cell damage at low temperatures. Deciduous trees shed their leaves and cease photosynthesizing. Many univoltine insects overwinter as early larvae inside egg cases. Many overwintering animal larvae make cryoprotectant to prevent cell damage from ice formation. The life cycle of a univoltine moth is shown in Figure 11.8A.

The ecological impact of seasonal dormancy is considerable. While endothermic vertebrates can exploit the winter environment by generating heat metabolically, ectothermic invertebrates—such as insects—are essentially unable to exploit the winter environment. Local sources of heat, such as decaying compost or hot springs, may occasionally allow insects to survive; but these insects are the exception. Thanks to dormancy, ectotherm species can flourish in northern circumpolar regions, greatly adding to their ecological diversity. Some endotherms, such as bears, exhibit **hibernation**, in which metabolic rate and body temperature fall. In some seasonal habitats, a similar dormancy pattern may occur in dry or hot summer periods, which is called **estivation**. A species does not have to be a ectotherm in order to use dormancy to get relief from climatic extremes.

A functional problem of seasonal dormancy occurs when winter temperatures rise to unusually high levels. Under these conditions, dormancy may be broken. If the dormant animal or plant experiences an increased metabolic rate, but does not feed, it may quickly run out of stored calories and starve to death (see Figure 11.8B). Selection will oppose breaking dormancy in this case, thus dormant overwintering is often cued to environmental signals that are more reliable than ambient temperature. Daylength is a common cue used by both plants and animals to control entry into dormancy as well as emergence from dormancy.

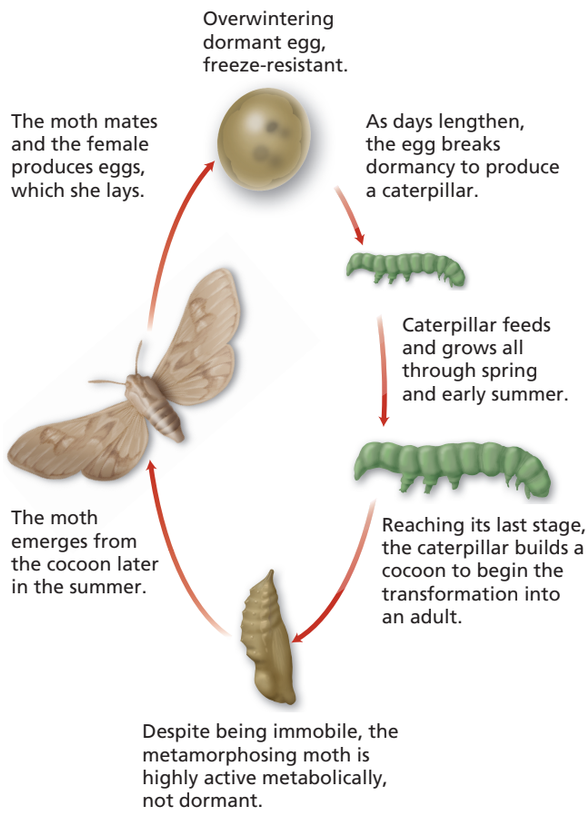


FIGURE 11.8A **The Life Cycle of a Univoltine Moth**

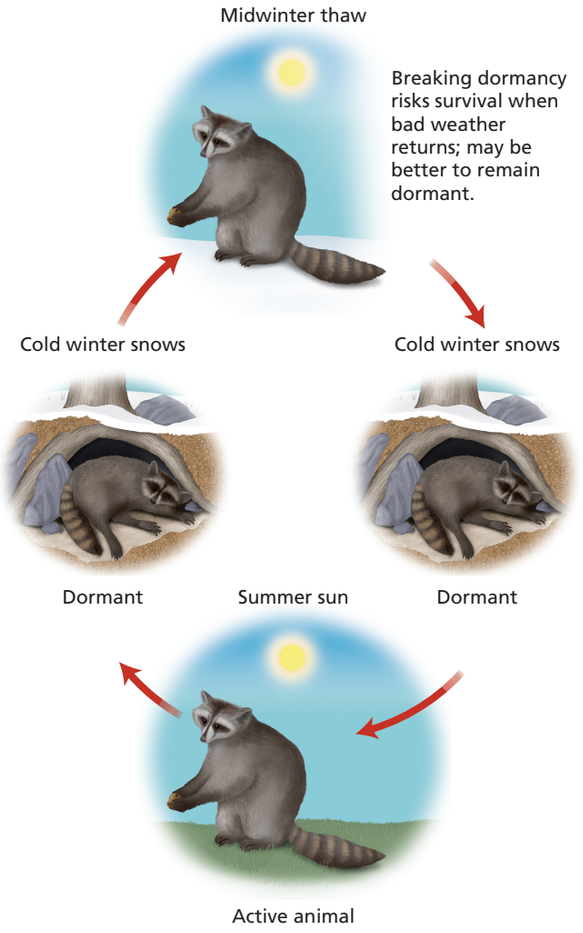


FIGURE 11.8B **Breaking Seasonal Dormancy**

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Many organisms have neither long-term nor seasonal dormancy, but show intermittent dormancy 11.9

If seeds provide a means to propagate through long periods of time, and seasonal dormancy allows species to utilize environments with extreme fluctuations, there are also temporary opportunities to use dormancy. Starvation is a common stress for animals, and some undergo dormancy or torpor during periods of reduced nutrition. The nematode *Caenorhabditis elegans* has a *dauer* stage that it enters partway through development, when conditions are stressful. As a dauer, the nematode greatly delays maturation to adulthood. An interesting feature of dauers is that they are not immobile; they move actively.

A somewhat similar case is nutritionally restricted rodents, both rats and mice, which greatly reduce their reproduction so long as food is restricted. However, these rodents have metabolic rates that are similar to those of well-fed rodents, in proportion to total body weight. They are also highly active, moving around with great fervor in their cages, unlike the superficially torpid, well-fed rodents. This entire syndrome is diagrammed in Figure 11.9A. It is important to understand that the effect of diet can be reversed. Reduced feeding converts a large ad lib rodent into an underweight healthier rodent, and vice versa.

A similar experiment was done on humans during the Biosphere II project (see Figure 11.9B). Biosphere II was intended as a mock-up of a colony on another planet, dependent on recycling its own resources. Food was grown within Biosphere II using materials within the facility, as well CO_2 and excrement from the humans. Due to an error in setting up the facility, there was not enough plant growth. Access to food was restricted for the Biosphereans, as it has been for experimental rodents. Slowly, the Biosphereans lost weight. As they did so, many indices of cardiovascular health improved. For example, blood pressure fell, the level of triglycerides (fat) in the blood fell, and serum cholesterol levels fell. It became very hard for the Biosphereans to work, and even harder to enjoy life. When the facility was opened, after years of reduced calories, all but one of the participants went off the restricted diet. Their cardiovascular health fell, their weight increased, and it became easier for them to function. In effect, they came out of dormancy.

In a number of species, dormancy may occur intermittently. The phenomenon of sleep in mammals can be seen as an example of temporary, marginal dormancy. Dormancy may take on a variety of forms, each form husbanding resources so that the organism can live long enough to develop or reproduce in good conditions. ❖

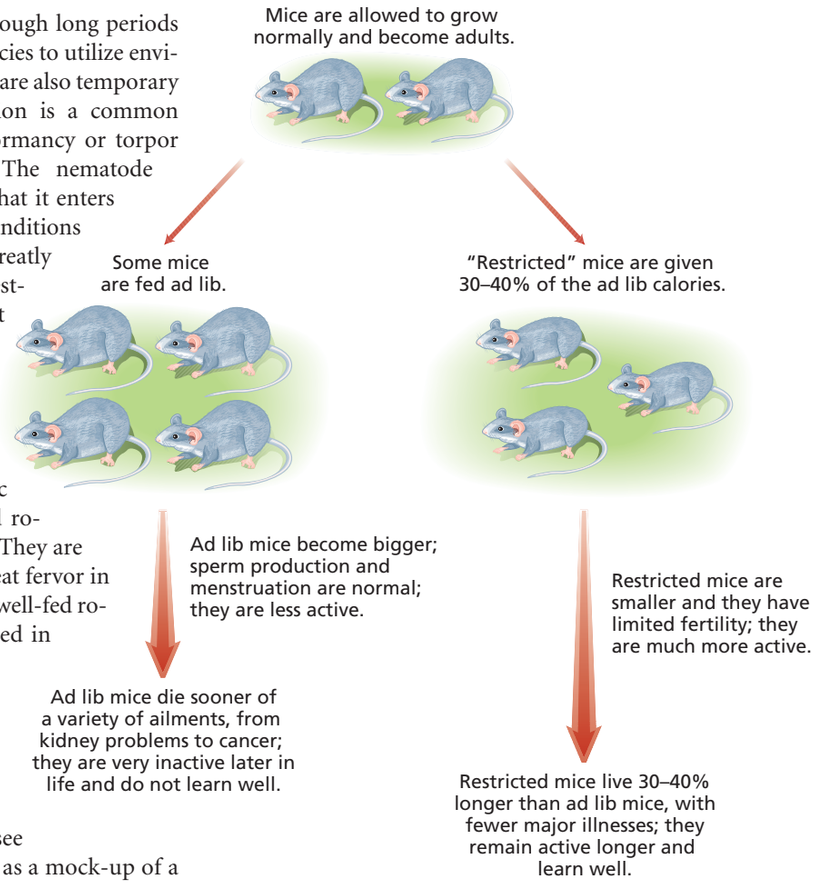


FIGURE 11.9A Restricted diets produce animals that reproduce little or not at all, while living longer. The best-known example of this pattern is caloric restriction in rodents, rats and mice particularly. Mice are used as an example.

FIGURE 11.9B **The Biosphere II Facility**

CONSEQUENCES OF DISPERSAL

11.10 Novel ecological structures: metapopulations

One way to appreciate the complexities of metapopulations is by studying a particularly good example. One such example is the metapopulations of the Glanville fritillary, *Melitaea cinxia* (a fritillary is just a spotted butterfly). This metapopulation, which has been studied extensively by Ilkka Hanski and his colleagues, is located on an island in southwest Finland (Figure 11.10A). The adult females typically mate once and then lay several large batches of eggs on one of the two host plants that are available. Most of the local populations (solid dots in Figure 11.10A) are quite small, consisting of larvae from just a few egg batches.

Metapopulations can be characterized by several important attributes.

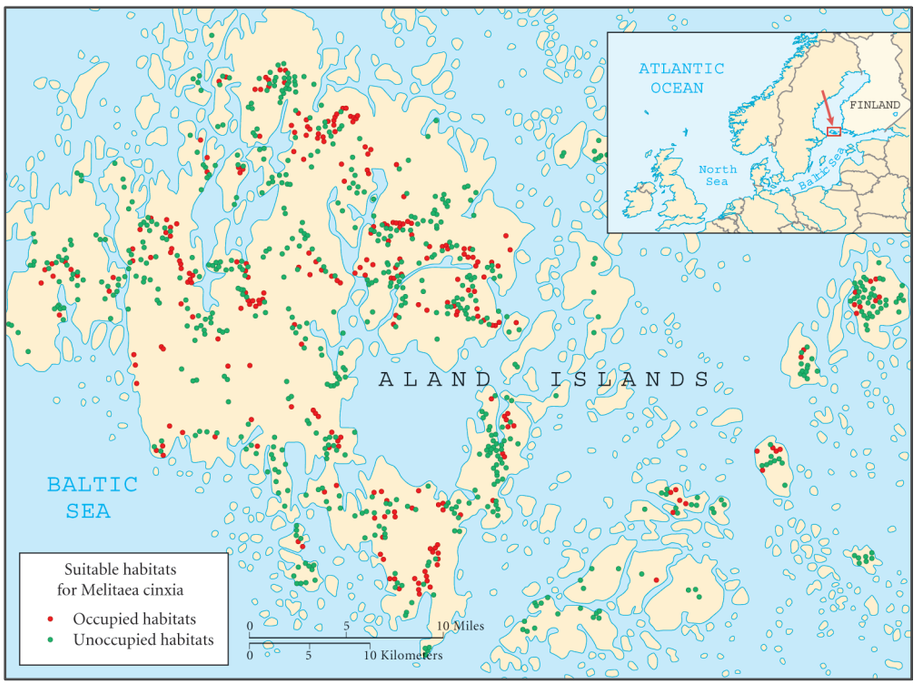


FIGURE 11.10A A Map of Åland Islands in Southwest Finland The circles show suitable habitats for *Melitaea cinxia*. The red circles are occupied habitats; the green circles are unoccupied.

1. They consist of spatially discrete breeding populations. This means that there must be purposeful movement or migration for individuals to get from one population to another.
2. All populations have a high risk of extinction. As a result, we expect to find at any time some suitable habitats that are unoccupied due to a recent extinction.
3. Recolonization of an extinct population is possible. This prevents the rapid extinction of the entire metapopulation.
4. There is asynchrony in local dynamics. While some populations have large numbers, others will be close to extinction. These types of fluctuations are not strongly correlated from one population to the next.

The Glanville fritillary has all four of these important metapopulation attributes.

As the area of patches increases, there should be more resources, and the patch should be able to support more individuals. Consequently, we expect extinctions to be less frequent when larger patches are occupied. This is exactly what has been observed in the Glanville fritillary (Figure 11.10B). In this metapopulation individuals do not move far when they migrate (Figure 11.10C), so it is not at all unusual for some populations not to receive any migrants for some time after they

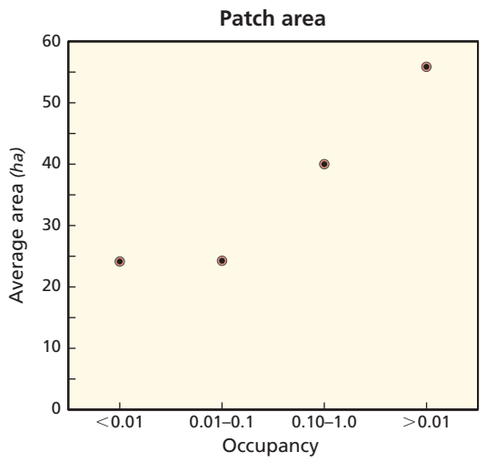
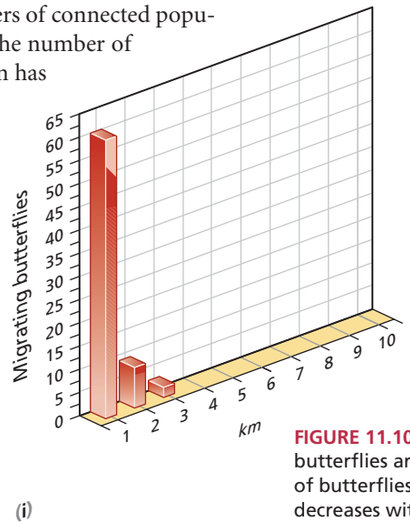


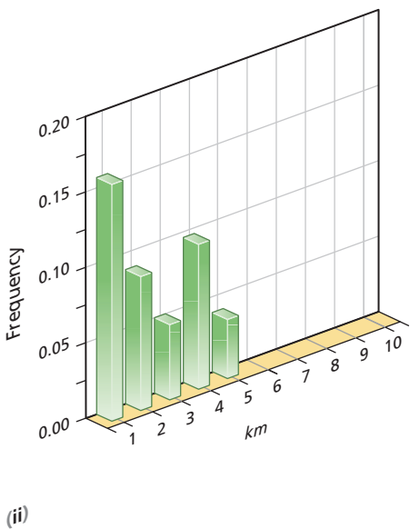
FIGURE 11.10B As patch area increases, the fraction of patches occupied also increases.

have gone extinct. This gives rise to the unoccupied patches, which are fairly frequent (Figure 11.10A).

Under what conditions would a whole metapopulation go extinct? It would seem plausible that if a metapopulation had very few connected populations, or **a small network**, then the chances of all going extinct simultaneously would be greater than if there were very large numbers of connected populations. The relationship between the number of patches in a network and extinction has been examined in the Glanville fritillary (Figure 11.10D). Hanski has concluded from these observations that a metapopulation should have 20 or more well-connected populations in order to be reasonably certain of prolonged persistence.



(i)



(ii)

FIGURE 11.10C In the Glanville fritillary, most migrating butterflies are found within 1 km of their home (i). The number of butterflies that successfully migrate to a new population decreases with distance between the two populations (ii).

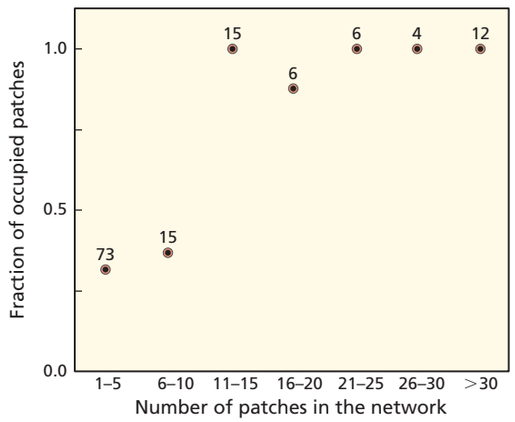
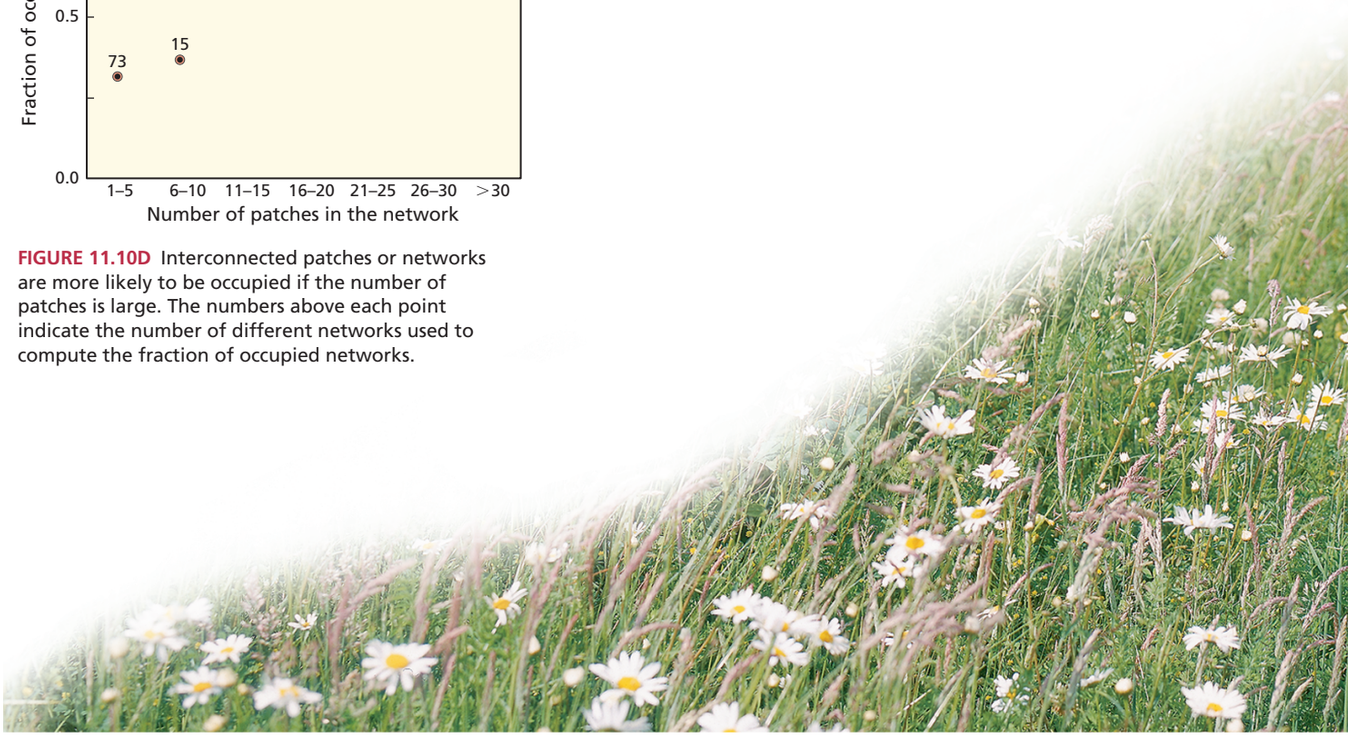


FIGURE 11.10D Interconnected patches or networks are more likely to be occupied if the number of patches is large. The numbers above each point indicate the number of different networks used to compute the fraction of occupied networks.



11.11 Connecting the genetics of populations: gene flow

We have already seen how migration can prevent population extinction. From a genetic perspective, the equivalent of extinction is the loss of genetic variation. The loss of genetic variation due to genetic drift can also be prevented by migration. In Figure 11.11A we have represented a group of small populations, all with two alleles called *A* and *a*. The *A* allele is shown as red and the *a* allele is blue. If these populations are completely isolated, then over many generations we expect either the *A* or *a* allele to be lost from each population. Which allele is lost is random, but it is certain to happen if we wait long enough. At the point when all populations have become fixed for just a single allele, there will be no heterozygotes in any populations (Figure 11.11A; Module 3.23).

Migration involves the movement of subsequent breeding of individuals from one population to the another. If migrants do not mate and have offspring, then their movement to a population will have no direct genetic consequences. The effects of migration on population differentiation will depend on both the migration rate (*m*, Figure 11.11A) and the population size, *N*. The forces of drift and migration work in opposite directions. Drift will tend to eliminate genetic variation; and the smaller the population, the faster the rate of elimination. Migration will generally reintroduce genetic variation, thus preventing its loss. Eventually these two forces will balance each other. An equilibrium level of heterozygosity will be reached that is equal to

$$2pq(4Nm)/(4Nm + 1).$$

As an example, consider the case where the two alleles have the same frequency, 0.5. The Hardy-Weinberg expectation is that heterozygotes will be 50 percent of each population. The drift and no-migration expectation is for 0 percent heterozygotes. In a population with just a 2 percent (0.02) migration rate and a population size of 1,000, the equilibrium frequency of heterozygotes should be 49.4 percent—very close to the Hardy-Weinberg expectation.

Is it possible to estimate the *N* and *m* for real populations? In fact, Montgomery Slatkin devised a method to estimate the product of *Nm* using a concept called **private alleles**. If genetic variation is measured in many subpopulations, private alleles are those found in only one of the subpopulations examined. If there is a lot of migration or drift is very weak, because the population size is large, it will be more difficult to establish private alleles in populations. This relationship is the core of Slatkin's method. In

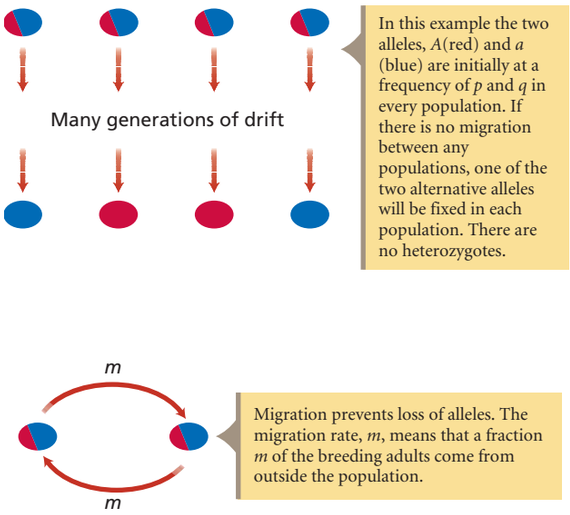


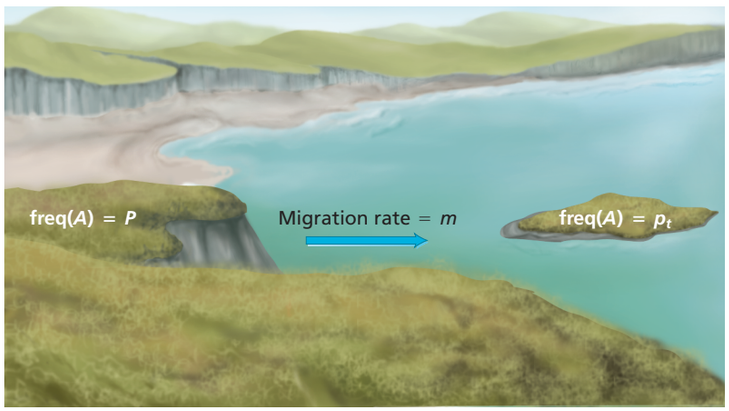
FIGURE 11.11A Migration and Population Differentiation

Table A. Estimates of gene flow (*Nm*) in several animal species.

Species	*Nm*
Marine mussel (*Mytilus edulis*)	42
Fruit fly (*Drosophila willistoni*)	9.9
Mouse (*Peromyscus californicus*)	2.2
Fruit fly (*Drosophila pseudoobscura*)	1.0
Pocket gopher (*Thomomys bottae*)	0.86
Mouse (*Peromyscus polionotus*)	0.31
Salamanders (*Plethoden cinereus*)	0.22

Table A we show estimates of Nm for several animal species. We see very high values for marine mussels. This seems reasonable since these organisms distribute their immature larval forms into the ocean, and the larvae may be carried great distances by ocean currents before they settle and become adults. Conversely, the salamander, *Plethodon cinereus*, includes samples from the southern United States, and as far north as Quebec, Canada. It is unlikely that a small terrestrial salamander can traverse even a small fraction of these distances. Therefore we expect small estimates of gene flow.

Another interesting example of migration occurs when there is essentially one-way flow from a large, mainland population to smaller, island populations (Figure 11.11B). In this case the migration affects allele frequencies only in the smaller population. In Figure 11.11B the frequency of an allele, A, is P on the mainland; and at time t, it is p_t on the island. If the migration rate from mainland to island is m, then the frequency of the A allele on the island changes each generation, as shown in Figure 11.11B. One application of this theory is to estimate the rate of gene flow between races in the United States. The U.S. African American population is much smaller than the U.S. Caucasian population and can be considered the island population in this theory. One allele in the Rh blood group is quite different in East Africans (0.63) and U.S. Caucasians (0.028). The allele's present frequency in the U.S. African American population is about 0.446. This suggests the frequency has been falling due to movement of Caucasian alleles into the African American population. If we assume that 300 or so years of African presence in the United States represents about 10 generations, then we can substitute values in the formula in Figure 11.11B to obtain the migration rate as $(0.446 - 0.028) = (1 - m)^{10}(0.63 - 0.028)$. After some algebra, we can find $m = 0.036$. This means that on average, about 3.6 percent of the alleles in the African American population come from U.S. Caucasians. After 10 generations this would mean about 30 percent of the African American alleles are from Caucasian ancestors. Using other genetic markers, estimates of gene flow into the U.S. African American population, or admixture, have been estimated at between 20 and 30 percent. ❖



After one generation
$p_{t+1} - P = (1 - m)(p_t - P)$
After n-generations
$p_{t+n} - P = (1 - m)^n(p_t - P)$

FIGURE 11.11B **Migration from a Large Mainland to an Island**

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SUMMARY

1. Animals and plants may move move or disperse from one location to another. These movements may be under the power of winds or currents, which is called passive dispersal, or under the organism's own power, called active dispersal.
2. More highly organized movements are called migrations.
3. Metapopulations are large numbers of discrete populations that are linked through migration.
4. The home ranges of animals are related to their environment and food requirements. Larger home ranges are required when resources are patchily distributed. Carnivores will generally require larger home ranges than herbivores will.
5. Organisms that cannot disperse may use dormancy as a means of escaping unfavorable conditions. Some organisms will become dormant for short periods of time. Others have a regular cycle of dormancy that coincides with the seasons. Still other organisms exhibit dormant phases that are released from dormancy by some special cue.
6. Metapopulations of butterflies show several general trends. The chance of patches being occupied increases with increasing patch area. The number of populations in the communicating network increases the chances of at least one patch being occupied. It seems at least 20 or more populations are required for a network to essentially be guaranteed of occupancy.
7. Even small amounts of migration are an effective means of preventing population differentiation.

REVIEW QUESTIONS

1. Discuss the different factors that affect home-range size.
2. How does upwelling and the Ekman flow affect barnacle recruitment?
3. What factors cause or release organisms from dormancy?
4. A mainland population has a common allele for brown eyes in an insect; the allele is at a frequency of 0.92. Migrants from this mainland arrive at a small island population and make up 3 percent of the breeding population in each generation. The brown-eye allele is at a frequency of only 0.1 on the island. What will the frequency of the brown-eye allele be after six generations of migration?

KEY TERMS

active dispersal
Coriolis effect
Eckman flow
estivation
hibernation
home range
indefinite dormancy
metapopulation
migration
network
outcross
passive dispersal
phytoplankton
polymorphic
private alleles
seasonal dormancy
seed bank
transient dormancy
upwelling

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