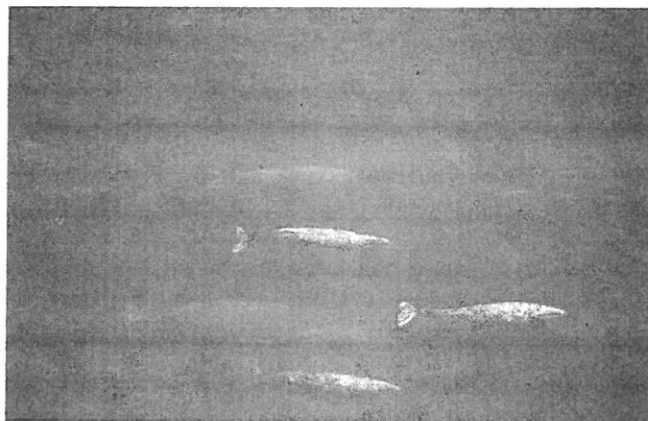


Standing on a headland in central California overlooking the Pacific Ocean, a small group of students spots a group of gray whales, *Eschrichtius robustus*, rising to the surface and spouting water as they swim northward (fig. 7.1a). The whales are rounding the point of land on their way to feeding grounds off the coasts of Alaska and Siberia. This particular group is made up of females and calves. The calves were born during the previous winter along the coast of Baja California, the gray whale's wintering grounds. Over the course of the spring, the entire population of over 20,000 gray whales will round this same headland on their way to the Bering and Chukchi Seas. Gray whales travel from one end of their range to the other twice each year, a distance of about 18,000 km. Home to the gray whale encompasses a swath of seacoast extending from southern Baja California to the coast of northeast Asia.

The grove of pine trees on the headland where the students stand gazing at the whales is winter home to another long distance traveler: monarch butterflies, *Danaus plexippus* (fig. 7.1b). The lazy flying of the bright orange and black monarch butterflies gives no hint of their capacity to migrate. Some of the butterflies flew to the grove of pines the previous autumn from as far away as the Rocky Mountains of southern Canada. As the students watch the whales, the male monarch butterflies pursue and mate with the female monarch butterflies. After mating, the males die, while the females begin a migration that leads inland and north. The females stop to lay eggs on any milkweeds they encounter along the way and eventually die; however, their offspring continue the migration. The monarch caterpillars grow quickly on their diet of milkweed and then transform to pupae contained within cocoons. The monarch butterflies that emerge from the cocoons mate and, like the previous generation, fly northward and inland. By moving farther north and inland each generation, some of the monarch butterflies eventually reach the Rocky Mountains of southern Canada, far from where their ancestors fluttered around the group of students on the pine-covered coastal headland.

Then as the autumn days grow shorter, the monarch butterflies begin their long flight back to the coastal grove of pines. This autumn generation, which numbers in the millions, flies southwest to their wintering grounds on the coast of central and southern California. Some of them might fly over 3,000 km. The monarch butterflies that survive the trip to the pine grove overwinter, hanging from particular roost trees in the thousands. They mate in the following spring and start the cycle all over again.

Gray whales and monarch butterflies, as different as they may appear, lead parallel lives. The Monterey pines, *Pinus radiata*, covering the headland where the monarch butterflies overwinter and by which the gray whales pass twice each year are quite different. The Monterey pine population does not migrate each generation and has a highly restricted distribution. The current natural range of the Monterey pine is limited to a few sites on the coast of central and northern California and to two islands off the coast of western Mexico. These scattered



(a)



(b)

FIGURE 7.1 (a) During their annual migration, the entire population of gray whales migrates from subtropical waters off Baja California to the Arctic and back again. (b) Some of the monarch butterflies roosting on these trees flew thousands of kilometers from the Rocky Mountains to reach their winter roost. In contrast, the entire natural population of the Monterey pine, *Pinus radiata*, is restricted to five small areas along the coast of California.

populations are the remnants of a large continuous population that extended for over 800 km along the California coast during the cooler climate of the last glacial period.

With these three examples, we begin to consider the ecology of populations. Ecologists usually define a **population** as a group of individuals of a single species inhabiting a specific area. A population of plants or animals might occupy a mountaintop, a river basin, a coastal marsh, or an island, all areas defined by natural boundaries. Just as often, the populations studied by biologists occupy artificially defined areas such as a particular country, county, or national park. The areas inhabited by populations range in size from the few cubic centimeters occupied by the bacteria in a rotting apple to the millions of square kilometers occupied by a population of migratory whales. A population studied by ecologists may consist of a highly localized group of individuals representing a fraction of the total population of a species, or it may consist of all the individuals of a species across its entire range.

Ecologists study populations for many reasons. Population studies hold the key to saving endangered species, controlling pest populations, and managing fish and game populations. They also offer clues to understanding and controlling disease epidemics. Finally, the greatest environmental challenge to biological diversity and the integrity of the entire biosphere is at its heart a population problem—the growth of the human population.

All populations share several characteristics. The first is its distribution. The distribution of a population includes the size, shape, and location of the area it occupies. A population also has a characteristic pattern of spacing of the individuals within it. It is also characterized by the number of individuals within it and their density, which is the number of individuals per unit area. Additional characteristics of populations—their age distributions, birth and death rates, immigration and emigration rates, and rates of growth—are the subject of the next two chapters. In this chapter we focus on two population characteristics: **distribution** and **abundance**.



CONCEPTS

- The physical environment limits the geographic distribution of species.
- On small scales, individuals within populations are distributed in patterns that may be random, regular, or clumped; on larger scales, individuals within a population are clumped.
- Population density declines with increasing organism size.
- Rarity is influenced by geographic range, habitat tolerance, and population size; rare species are vulnerable to extinction.



CASE HISTORIES: distribution limits



The physical environment limits the geographic distribution of species.

A major theme in chapters 4, 5, and 6 is that individual organisms have evolved physiological, anatomical, and behavioral characteristics that compensate for environmental variation. Organisms compensate for temporal and spatial variation in the environment by regulating body temperature and water content and by foraging in a way that maintains energy intake at relatively high levels. However, there are limits on how much organisms can compensate for environmental variation.

While there are few environments on earth without life, no single species can tolerate the full range of earth's environments. For each species some environments are too warm, too cold, too saline, or unsuitable in other ways. As we saw in chapter 6, organisms take in energy at a limited rate. It appears that at some point, the metabolic costs of compensating for environmental variation may take up too much of an organism's energy budget. Partly because of these energy constraints, the physical environment places limits on the distributions of populations. Let's now turn to some actual species and explore the factors that limit their distributions.

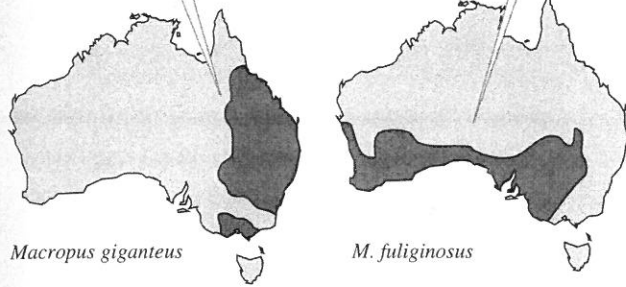
Kangaroo Distributions and Climate

The Macropodidea includes the kangaroos and wallabies, which are some of the best known of the Australian animals. However, this group of large-footed mammals includes many less familiar species, including rat kangaroos and tree kangaroos. While some species of macropods can be found in nearly every part of Australia, no single species ranges across the entire continent. All are confined to a limited number of climatic zones and biomes.

G. Caughley and his colleagues (1987) found a close relationship between climate and the distributions of the three largest kangaroos in Australia (fig. 7.2). The eastern grey kangaroo, *Macropus giganteus*, is confined to the eastern third of the continent. This portion of Australia includes several biomes (see chapter 2). Temperate forest grows in the southeast and tropical forests in the north. Mountains, with their varied climates, occupy the central part of the eastern grey kangaroo's range (see figs. 2.13, 2.28, and 2.37). The climatic factor that distinguishes these varied biomes is little seasonal variation in precipitation or dominance by summer precipitation. The western grey kangaroo, *M. fuliginosus*, lives mainly in the southern and western regions of Australia. Most of the western grey kangaroo's range coincides with the distribution of the temperate woodland and shrubland biome

Macropus giganteus lives in eastern Australia, where there is little seasonal variation in precipitation or dominance by summer precipitation.

M. fuliginosus lives in southern Australia, where winter rainfall dominates.



M. rufus lives in central and western Australia, where conditions are hot and dry.

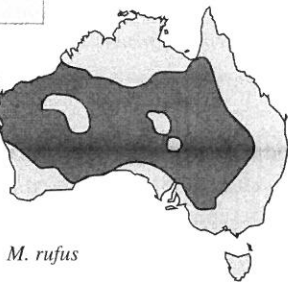


FIGURE 7.2 Climate and the distributions of three kangaroo species (data from Caughley et al. 1987).

in Australia. The climatically distinctive feature of this biome is a predominance of winter rainfall (see fig. 2.22). Meanwhile, the red kangaroo, *M. rufus*, wanders the arid and semiarid interior of Australia. The biomes that cover most of the red kangaroo's range are savanna and desert (see figs. 2.16 and 2.19). Of the three species of large kangaroos, the red kangaroo occupies the hottest and driest areas.

The distributions of these three large kangaroo species cover most of Australia. However, as you can see in figure 7.2, none of these species lives in the northernmost region of Australia. Caughley and his colleagues explain that these northern areas are probably too hot for the eastern grey kangaroo, too wet for the red kangaroo, and too hot in summer and too dry in winter for the western grey kangaroo. However, they are also careful to point out that these limited distributions may not be determined by climate directly. Instead, they suggest that climate often influences species distributions through factors such as food production, water supply, and habitat. Climate also affects the incidence of parasites, pathogens, and competitors.

Regardless of how the influences of climate are played out, the relationship between climate and the

distributions of species can be stable over long periods of time. The distributions of the eastern grey, western grey, and red kangaroos have been stable for at least a century. In the next example, we discuss a species of beetle that appears to have maintained a stable association with climate for 10,000 to 100,000 years.

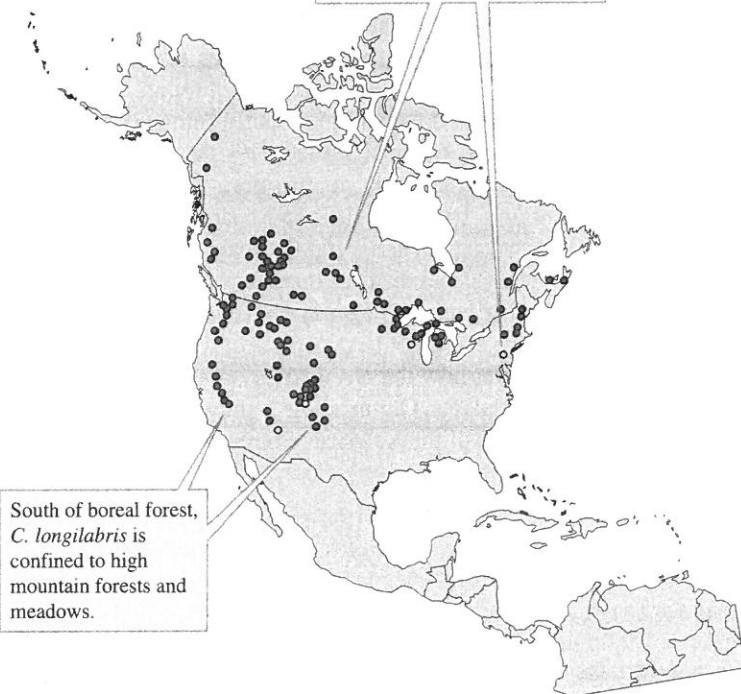
A Tiger Beetle of Cold Climates

Tiger beetles have entered our discussions several times. In chapter 4, we saw how one species regulates body temperatures on hot black beaches in New Zealand. In chapter 5, we compared the water loss rates of tiger beetles from desert grasslands and riparian habitats in Arizona. Here we consider the distribution of a tiger beetle that inhabits the cold end of the range of environments occupied by tiger beetles.

The tiger beetle *Cicindela longilabris* lives at higher latitudes and higher elevations than just about any other species of tiger beetle in North America. In the north, *C. longilabris* is distributed from the Yukon Territory in northwestern Canada to the maritime provinces of eastern Canada (fig. 7.3). This

The distribution of the tiger beetle *C. longilabris*, across North America suggests that it is confined to cool, moist habitats.

In the far north, *C. longilabris* lives throughout the boreal forests of North America.



South of boreal forest, *C. longilabris* is confined to high mountain forests and meadows.

FIGURE 7.3 A tiger beetle, *Cicindela longilabris*, confined to cool environments (data from Schultz, Quinlan, and Hadley 1992).

northern band of beetle populations coincides with the distribution of northern temperate forest and boreal forest in North America (see figs. 2.28 and 2.30). *C. longilabris* also lives as far south as Arizona and New Mexico. However, these southern populations are confined to high mountains, where *C. longilabris* is associated with montane coniferous forests. As we saw in chapter 2, these high mountains have a climate similar to that of boreal forest (see fig. 2.38).

Ecologists suggest that during the last glacial period *C. longilabris* lived far south of its present range limits. Then with climatic warming and the retreat of the glaciers, the tiger beetles followed their preferred climate northward and up in elevation into the mountains of western North America (fig. 7.3). As a consequence, the beetles in the southern part of this species range live in isolated mountaintop populations. This hypothesis is supported by the fossil records of many beetle species.

Intrigued by the distribution and history of *C. longilabris*, Thomas Schultz, Michael Quinlan, and Neil Hadley (1992) set out to study the environmental physiology of widely separated populations of the species. Populations separated for many thousands of years may have been exposed to significantly different environmental regimes. If so, natural selection could have produced significant physiological differences among populations. The researchers compared the physiological characteristics of beetles from populations of *C. longilabris* from Maine, Wisconsin, Colorado, and northern Arizona. Their measurements included water loss rates, metabolic rates, and body temperature preferences.

Schultz and his colleagues found that the metabolic rates of *C. longilabris* are higher and its preferred temperatures lower than those of most other tiger beetle species that have been studied. These differences support the hypothesis that *C. longilabris* is adapted to the cool climates of boreal and montane forests. In addition, the researchers found that none of their measurements differed significantly among populations of *C. longilabris*. Figure 7.4 illustrates the remarkable similarity in preferred body temperature shown by foraging *C. longilabris* from populations separated by as much as 3,000 km and, perhaps, by 10,000 years of history. These results support the generalization that the physical environment limits the distributions of species. It also suggests that those limits may be stable for long periods of time.

Now, let's consider how the physical environment may limit the distribution of plants. Our example is drawn from the arid and semiarid regions of the American Southwest.

Distributions of Plants Along a Moisture-Temperature Gradient

In chapter 4, we discussed the influence of pubescence on leaf temperature in plants of the genus *Encelia*. Variation in leaf pubescence among *Encelia* species appears to correspond directly to the distributions of these species along a moisture-

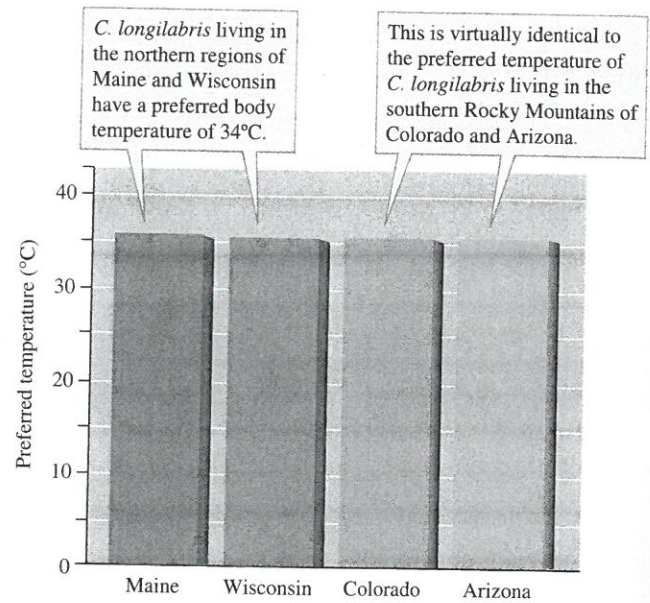


FIGURE 7.4 Uniform temperature preference across an extensive geographic range (data from Schultz, Quinlan, and Hadley 1992).

temperature gradient from the California coast eastward (Ehleringer and Clark 1988). *Encelia californica*, the species with the least pubescent leaves, occupies a narrow coastal zone that extends from southern California to northern Baja California (fig. 7.5). Inland, *E. californica* is replaced by *E. actoni*, which has leaves that are slightly more pubescent. Still farther to the east, *E. actoni* is in turn replaced by *E. frutescens* and *E. farinosa*.

These geographic limits to these species' distributions correspond to variations in temperature and precipitation. The coastal environments where *E. californica* lives are all relatively cool. However, average annual precipitation differs a great deal across the distribution of this species. Annual precipitation ranges from about 100 mm in the southern part of its distribution to well over 400 mm in the northern part. By comparison, *E. actoni* occupies environments that are only slightly warmer but considerably drier. The rainfall in areas occupied by *E. frutescens* and *E. farinosa* is similar to the amount that falls in the areas occupied by *E. actoni* and *E. californica*. However, the environments of *E. frutescens* and *E. farinosa* are much hotter.

Variation in leaf pubescence does not correspond entirely to the macroclimates inhabited by *Encelia* species. The leaves of *E. frutescens* are nearly as free of pubescence as the coastal species *E. californica*. However, *E. frutescens* grows side by side with *E. farinosa* in some of the hottest deserts in the world. Because they are sparsely pubescent, the leaves of *E. frutescens* absorb a great deal more radiant energy than the leaves of *E. farinosa* (fig. 7.6). Under similar conditions, however, leaf temperatures of the two species are nearly identical. How does *E. frutescens* avoid overheating? The leaves do not overheat because they transpire at a high rate and are evaporatively cooled as a consequence.

tions, biological factors may be as important or even more important than physical factors in determining the distribution and abundance of species. Often the influences of biological factors remain hidden, however, because of the difficulty of demonstrating them. In ecology, we must usually probe deeper to see beyond outward appearances, as Connell did when he transplanted *Chthamalus* from the upper to the lower intertidal zone. The influence of biological factors, such as competition, predation, and disease, on the distribution and abundance of organisms is a theme that enters our discussions frequently in the remainder of this book, especially in chapters 10, 11, and 12.

CASE HISTORIES: distribution patterns

Start

On small scales, individuals within populations are distributed in patterns that may be random, regular, or clumped; on larger scales, individuals within a population are clumped.

We have just considered how the environment limits the distributions of species. When you map the distribution of a species such as the red kangaroo in Australia (see fig. 7.2), or the zoned distribution of *Chthamalus* and *Balanus* in the intertidal zone (see fig. 7.8), the boundaries on your map indicate the range of the species. In other words, your map shows where at least some individuals of the species live and where they are absent. Knowing a species' range, as defined by presence and absence, is useful, but it says nothing about how the individuals that make up the population are distributed in

the areas where they are present. Are individuals randomly distributed across the range? Are they regularly distributed? As we shall see, the distribution pattern observed by an ecologist is strongly influenced by the scale at which a population is studied.

Ecologists refer frequently to large-scale and small-scale phenomena. What is "large" or "small" depends on the size of organism or other ecological phenomenon under study. For this discussion, **small scale** refers to distances of no more than a few hundred meters, over which there is little environmental change significant to the organism under study. **Large scale** refers to areas over which there is substantial environmental change. In this sense, large scale may refer to patterns over an entire continent or patterns along a mountain slope, where environmental gradients are steep. Let's begin our discussion with patterns of distribution observed at small scales.

Distributions of Individuals on Small Scales

Three basic patterns of distribution are observed on small scales: random, regular, or clumped. A **random distribution** is one in which individuals within a population have an equal chance of living anywhere within an area. A **regular distribution** is one in which individuals are uniformly spaced. In a **clumped distribution**, individuals have a much higher probability of being found in some areas than in others (fig. 7.10).

These three basic patterns of distribution are produced by the kinds of interactions that take place between individuals within a population, by the structure of the physical environment, or by a combination of interactions and environmental structure. Individuals within a population may *attract* each other, *repel* each other, or *ignore* each other. Mutual attraction

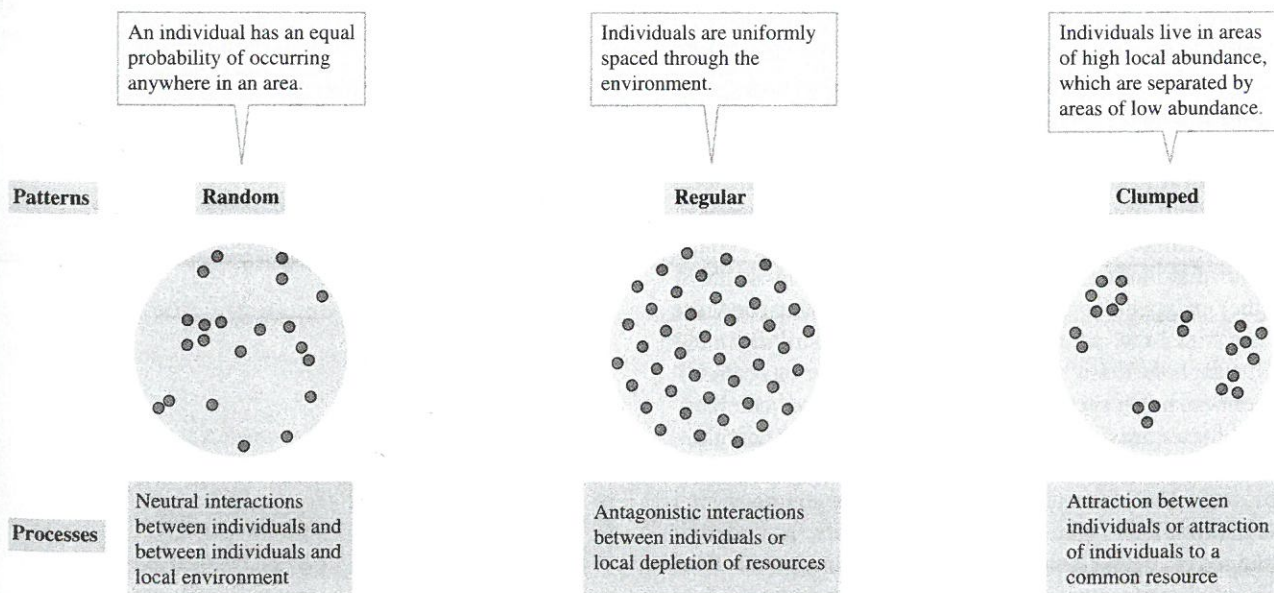


FIGURE 7.10 Random, regular, and clumped distributions.

creates clumped, or aggregated, patterns of distribution. Regular patterns of distribution are produced when individuals avoid each other or claim exclusive use of a patch of landscape. Neutral responses contribute to random distributions.

The patterns created by social interactions may be reinforced or damped by the structure of the environment. An environment with patchy distributions of nutrients, nesting sites, water, and so forth fosters clumped distribution patterns. An environment with a fairly uniform distribution of resources and frequent, random patterns of disturbance (or mixing) tends to reinforce random or regular distributions. Let's now consider factors that influence the distributions of some species in nature.

Distributions of Tropical Bee Colonies

Stephen Hubbell and Leslie Johnson (1977) recorded a dramatic example of how social interactions can produce and enforce regular spacing in a population. They studied competition and nest spacing in populations of stingless bees in the family Trigonidae. The bees they studied live in tropical dry forest in Costa Rica. Though these bees do not sting, rival colonies of some species fight fiercely over potential nesting sites.

Stingless bees are abundant in tropical and subtropical environments, where they gather nectar and pollen from a wide variety of flowers. They generally nest in trees and live in colonies made up of hundreds to thousands of workers. Hubbell and Johnson observed that some species of stingless bees are highly aggressive to other members of their species from other colonies, while others are not. Aggressive species usually forage in groups and feed mainly on flowers that occur in high-density clumps. The nonaggressive species feed singly or in small groups and on more widely distributed flowers.

Hubbell and Johnson studied several species of stingless bees to determine whether there is a relationship between aggressiveness and patterns of colony distribution. They predicted that the colonies of aggressive species would show regular distributions while those of nonaggressive species would show random or clumped distributions. They concentrated their studies on a 13 ha tract of tropical dry forest that contained numerous nests of nine species of stingless bees.

Though Hubbell and Johnson were interested in how bee behavior might affect colony distributions, they recognized that the availability of potential nest sites for colonies could also affect distributions. So, in one of the first steps in their study, they mapped the distributions of trees suitable for nesting. They found that potential nest trees were distributed randomly through the study area and that the number of potential nest sites was much greater than the number of bee colonies. What did these measurements tell the researchers? They indicated that the number of colonies in the study area was not limited by availability of suitable trees and that clumped and regular distribution of colonies would not be due to an underlying clumped or regular distribution of potential nest sites.

Hubbell and Johnson were able to map the nests of five of the nine species of stingless bees accurately. The nests of

four of these species were distributed regularly. As they had predicted, all four species with regular nest distributions were highly aggressive to bees from other colonies of their own species. The fifth species, *Trigona dorsalis*, was not aggressive and its nests were randomly distributed over the study area. Figure 7.11 contrasts the random distribution of *T. dorsalis* with the regular distribution of one of the aggressive species, *T. fulviventris*.

The researchers also studied the process by which the aggressive species establish new colonies. In the process, they made observations that provide insights into the mechanisms that establish and maintain the regular nest distributions of species such as *T. fulviventris*. This species and the other aggressive species apparently mark prospective nest sites with a pheromone. **Pheromones** are chemical substances secreted by some animals for communication with other members of their species. The pheromone secreted by these stingless bees attracts and aggregates members of their colony to the prospective nest site; however, it also attracts workers from other nests.

If workers from two different colonies arrive at the prospective nest, they may fight for possession. Fights may be escalated into protracted battles. Hubbell and Johnson observed battles over a nest tree that lasted for 2 weeks. Each dawn, 15 to 30 workers from two rival colonies arrived at the contested nest site. The workers from the two rival colonies faced off in two swarms and displayed and fought with each other. In the displays, pairs of bees faced each other, slowly flew vertically to a height of about 3 m, and then grappled each other to the ground. When the two bees hit the ground, they separated, faced off, and performed another aerial display. Bees did not appear to be injured in these fights, which

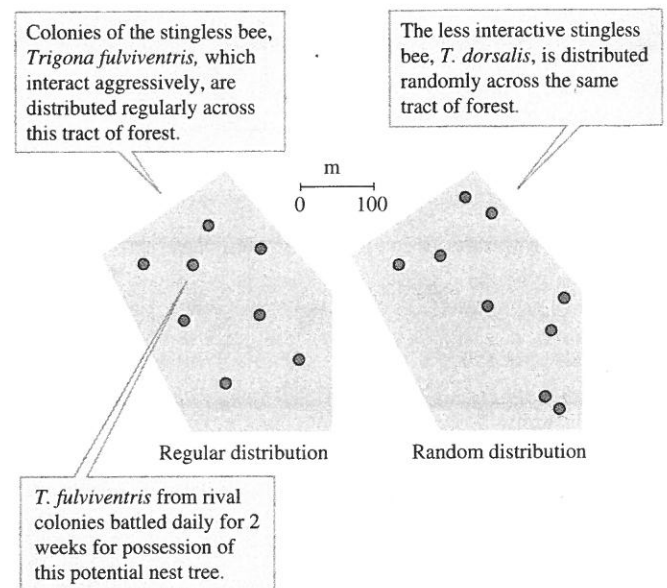


FIGURE 7.11 Regular and random distributions of stingless bee colonies in the tropical dry forest (data from Hubbell and Johnson 1977).

were apparently ritualized. The two swarms abandoned the battle at about 8 or 9 A.M. each morning, only to re-form and begin again the next day just after dawn. While this contest over an unoccupied nest site produced no obvious mortality, fights over occupied nests sometimes killed over 1,000 bees in a single battle. These tropical bees space their colonies by engaging in pitched battles, but as we see next, plants space themselves by more subtle means.

Distributions of Desert Shrubs

Stop

Half a century ago desert ecologists suggested that desert shrubs tend to be regularly spaced due to competition between the shrubs. You can see the patterns that inspired these early ecologists by traveling across the seemingly endless expanses of the Mojave Desert in western North America. One of the most common plants that you will see is the creosote bush, *Larrea tridentata*, which dominates thousands of square kilometers of this area. As you look out across landscapes dominated by creosote bushes it may appear that the spacing of these shrubs is regular (fig. 7.12). In places, their spacing is so uniform that they appear to have been planted by some very careful gardener. As we shall see, however, visual impressions can be deceiving.

Quantitative sampling and statistical analysis of the distributions of creosote bushes and other desert shrubs led to a controversy that took the better part of two decades to settle. In short, when different teams of researchers quantified the distributions of desert shrubs, some found the regular distributions reported by earlier ecologists. Others found random or clumped distributions. Still others reported all three types of distributions.

Though we are generally accustomed to having one answer to our questions, the answers to ecological questions are often more complex. Research by Donald Phillips and James MacMahon (1981) showed that the distribution of creosote bushes changes as they grow. They mapped and analyzed the distributions of creosote bushes and several other shrubs at

nine sites in the Sonoran and Mojave Deserts. Because earlier researchers had suggested that creosote bush spacing changed with available moisture, they chose sites with different average precipitations. Precipitation at the study sites ranged from 80 to 220 mm, and average July temperature varied from 27° to 35°C. Phillips and MacMahon took care to pick sites with similar soils and with similar topography. They studied populations growing on sandy to sandy loam soils with less than 2% slope with no obvious surface runoff channels.

The results of this study indicate that the distribution of desert shrubs changes from clumped to random to regular distribution patterns as they grow. The young shrubs tend to be clumped for three reasons: because seeds germinate at a limited number of "safe sites," because seeds are not dispersed far from the parent plant, or because asexually produced offspring are necessarily close to the parent plant. Phillips and MacMahon proposed that as the plants grow, some individuals in the clumps die, which reduces the degree of clumping. Gradually, the distribution of shrubs becomes more and more random. However, competition among the remaining plants produces higher mortality among plants with nearby neighbors, which thins the stand of shrubs still further and eventually creates a regular distribution of shrubs. This hypothetical process is summarized in figure 7.13.

Phillips and MacMahon and other ecologists proposed that desert shrubs compete for water and nutrients, a competition that takes place belowground. How can we study these belowground interactions? Work by Jacques Brisson and James Reynolds (1994) provides a quantitative picture of the belowground side of creosote bush distributions. These researchers carefully excavated and mapped the distributions of 32 creosote bushes in the Chihuahuan Desert. They proposed that if creosote bushes compete, their roots should grow in a way that reduces overlap with the roots of nearby individuals.

The 32 excavated creosote bushes occupied a 4 by 5 m area on the Jornada Long Term Ecological Research site near Las Cruces, New Mexico. The creosote bush was the only shrub within the study plot. Their roots penetrated to only 30 to 50 cm, the depth of a hardpan calcium carbonate deposition layer. Because they did not have to excavate to great depths, Brisson and Reynolds were able to map more root systems than previous researchers. Still, their excavation and mapping of roots required 2 months of intense labor.

The complex pattern of root distributions uncovered confirmed the researchers proposal: Creosote bush roots grow in a pattern that reduces overlap between the roots of adjacent plants (fig. 7.14a). We can make the root distributions of individual plants clearer by plotting their perimeters only. Figure 7.14b shows the hypothetical distributions of creosote bushes with circular root systems, while figure 7.14c shows their actual root distributions. Notice that the root systems of creosote bushes overlap much less than they would if they had circular distributions. Brisson and Reynolds conclude that competitive interactions with neighboring shrubs influence the distribution of creosote bush roots. Their work suggests that creosote bushes compete for belowground resources.



FIGURE 7.12 Are local populations of the creosote bush, *Larrea tridentata*, distributed regularly?