

PART THREE

THE DARWINIAN ORGANISM



How organisms function cannot be understood just by studying molecules or cells. The organism is more than the sum of its parts. For instance, regulation of body temperature often depends on behavior. Butterflies spread open their wings in direct sunlight to

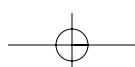
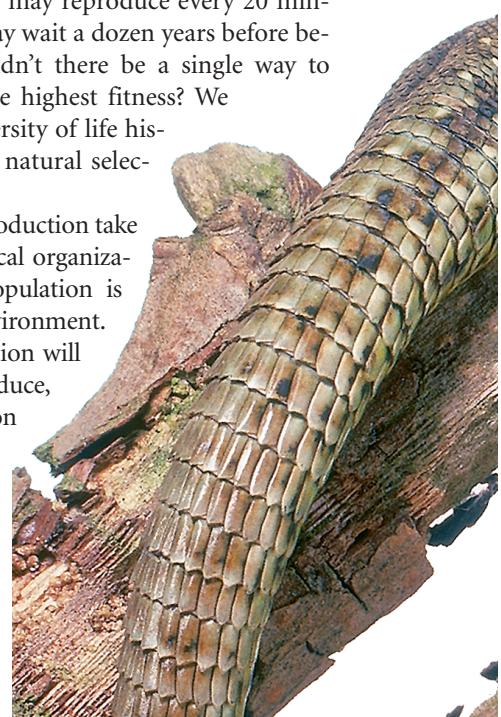
warm themselves. Lizards raise their body temperatures by resting on rock surfaces that have been warmed by the sun. The integration of physiology and behavior makes thermoregulation possible in these animals. This is only one example of the many ways in which organismal biology is integrated with ecology and evolution.

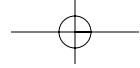
It is possible to study organismal function and physiology by simply studying how the organism works as a biochemical machine. The effect of temperature on the rate of an organism's biochemical reactions can be studied by itself, as can the biochemical reactions of organisms to extreme heat. But this will not provide us with a complete understanding of how the organism regulates its temperature. We gain deeper insights into organismal biology if we remember that natural selection has had a hand in determining how organisms function. Thus the term the *Darwinian organism*, because the way organisms function is partly the product of natural selection acting in a particular ecological context. Butterflies that have evolved "sunning" behavior are better equipped to survive in cooler environments, and therefore they are favored by natural selection. In general, the process of natural selection molds behaviors and functions in ways that help the organisms regulate their physiology. Scientists are now performing experiments in which they can observe the evolution of important physiological functions. We introduce you to this work in Chapter 9.

Organisms also reproduce, and as *Darwinian* organisms this is their most important function. It should come as no

surprise that most aspects of reproduction are under the influence of natural selection. However, the ways organisms reproduce are quite variable. A goal of Chapter 7 is to help you understand why all organisms are not identical with respect to the timing and duration of reproduction. How do we make sense of the fact that bacteria may reproduce every 20 minutes, while large mammals may wait a dozen years before beginning reproduction? Shouldn't there be a single way to reproduce that always has the highest fitness? We can understand the great diversity of life histories by understanding how natural selection acts on reproduction.

The consequences of reproduction take us to the next level of biological organization, the population. The population is part of the individual's environment. The composition of a population will change as organisms reproduce, which in turn sets into motion the conditions for evolutionary change. A change in the composition or size of an



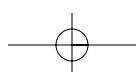
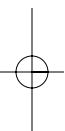
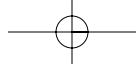


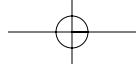
organism's population is like changing temperature, food availability, or any other aspect of the ecological environment. As the number of organisms in a population increases, there will be effects on reproduction. This will alter the effect of natural selection on the traits of organisms, as well as changing the ecology of the whole population. This connection between evolution at the level of the organism and changes in the ecology of whole populations is one of the more fascinating aspects of the Darwinian organism. In Chapter 10 we review how populations grow, and how evolution affects population dynamics.

Populations of animals and plants are not static in space. We see movements of populations, as with the migration of birds during the winter. Even when individuals cannot move, their gametes may. Plants often have elaborate methods for ensuring the wide dispersal of seeds. In Chapter 11 we discuss the importance of dispersal.

After reading Chapters 7 through 11, you should be able to start thinking in Darwinian terms. When interpreting behavior, physiology, or life cycles, you will naturally ask if they have adaptive aspects. These questions help make sense out of the great complexity of biological diversity.







7

Reproduction is costly, as illustrated by the near-simultaneity of reproduction and death in Pacific salmon.



Life History of the Organism

The Pacific salmon leaping up the waterfall is on its way to spawn and then die. For this bony fish, dying and reproducing have a poignant simultaneity. Yet there is much about its life history that is universal. The cycle of birth, reproduction, and death is basic to all organisms, even when the specific features of these life histories vary. Plants disperse pollen. Some animals make their way into the world by cracking open their eggshell, while others struggle to emerge from their mother's body during birth. Some unicellular life-forms and some simple animals just split in two, and the two halves become separate organisms right away. There is great diversity among life cycles.

One thing is unitary to all these life histories: Darwinian fitness, the net reproduction of individual organisms. And fitness in turn is defined by the life history. There are two main ways in which fitness is determined: (1) the product of viability and

fertility; and (2) the integration of survival and reproduction over a complex life cycle. We will show how these two kinds of fitness arise, what they mean, and what their consequences are for the life cycle of the organism.

The focus of fitness is reproduction, the key point of every life history. Thinking about life histories in relation to net reproduction gives a useful focus on how life histories evolve. An important thing about reproduction is that, even though it is essential to Darwinian fitness, it may be destructive for the individual organism. Reproduction has costs, and these costs limit its evolution.

If the initiation of new lives is obviously important for any life history, there is also the end of life to consider—death. Death comes in an unrelenting form at advanced ages, through a loss of health and vigor known to us as aging. Aging is a unifying theme of life histories, though it is not universal.♦

FITNESS AND LIFE HISTORIES

7.1 There are many types of life history

Bacteria have one reproductive episode. Once the cell is ready to divide, it divides exactly once, and then there are two immature cells. Adults do not exist. This is the essential feature of these life histories. Organisms are either developing toward reproduction or reproducing. There is no adult phase between reproductive events.

Bacteria are not the only organisms like this. Many single-celled organisms reproduce by fission—and even some multicellular animals, such as asexual sea anemone species. Figure 7.1A shows some examples.

But having just one reproductive episode does not require fission. Insects that have one generation per year are described as **univoltine**, and they also have one reproductive episode. Examples of univoltine insects are particularly common among the butterflies and moths of temperate North America. In spring, caterpillars hatch out of eggs that have overwintered on a tree branch or on the ground. The caterpillars are quite small at first. Over successive molts, the caterpillars grow substantially. They then form a pupa, in which they undergo a metamorphosis to the adult moth morphology. The adults mate after emerging from the pupa. The females lay their eggs, in a clump or dispersed

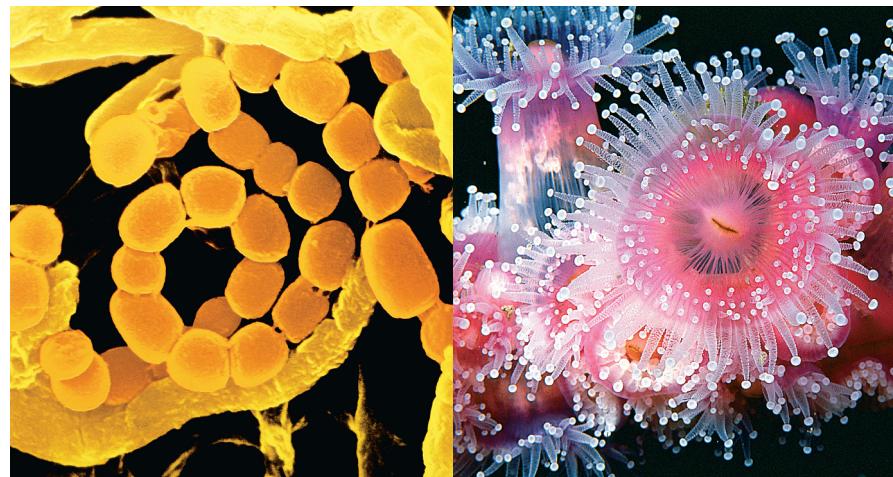


FIGURE 7.1A Bacteria (left) and Sea Anemones (right)

over host plants, and then die. The cycle then begins again next spring.

Among animals generally, this type of **life history** is called **semelparous**. An interesting point is that semelparous life histories do not have to be annual. The 13-year and 17-year cicadas have a similar pattern of semelparous reproduction, except that in their case the cycle has a length of 13 or 17 years, from the start of one adulthood to the start of the adulthood of the offspring.

Many plants have a growth cycle that is termed **annual**, although some annual plants may survive into the next growing season. **Monocarpic** plants, such as soybean, have a strictly semelparous life history; the adult plants die right after reproducing.

Male marsupial “mice,” *Antechinus stuartii*, an Australian species unrelated to mice elsewhere, also have semelparous reproduction. Just before the start of the mating season, the males undergo profound hormonal changes. They become more aggressive and their genitals enlarge. Come mating time, males fight with each other and copulate with females for hours at a time. They lose weight, suffer numerous internal lesions, and lose resistance to parasites. Once the mating season is over, the males die very quickly. None make it to the next mating season. Some females, interestingly, do make it to the next reproductive season, like “annual” plants do. Apparently reproduction is more stressful for males in this species. Figure 7.1B shows a cicada, Figure 7.1C shows a field of soybean, and Figure 7.1D shows a marsupial mouse.

Most of the organisms that we are familiar with have a pattern of repeated, or **iteroparous**, reproduction. We have such a pattern ourselves. Most

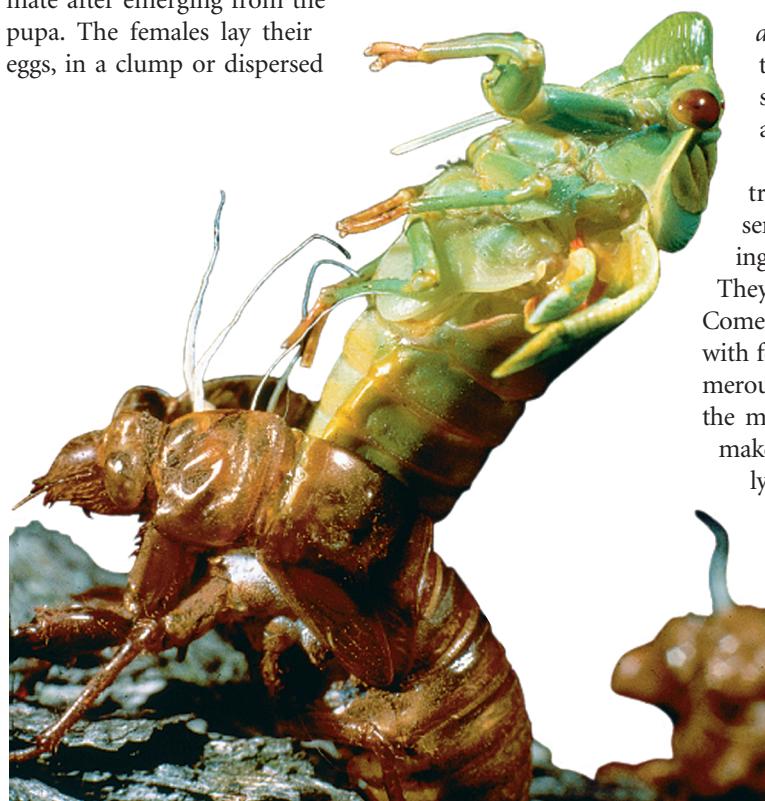


FIGURE 7.1B A Cicada molting



FIGURE 7.1C Field of Soybeans

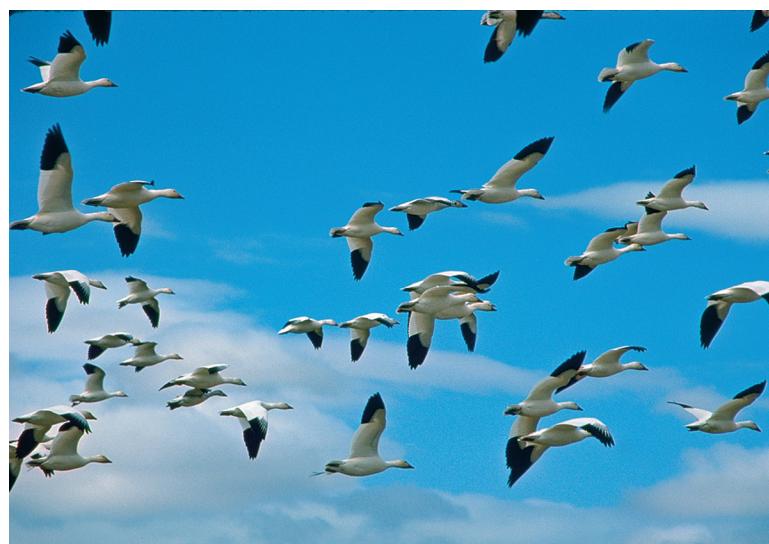


FIGURE 7.1E Snow Geese

mammals, birds, and reptiles have adult stages that can reproduce more than once, sometimes with long periods of time between each reproductive event.

Just as semelparous species often time their reproduction to the annual cycle of seasons, so do some repeated reproducers produce offspring once a year, at about the same calendar dates. But with iteroparous reproducers, some reproduce again the next year, and possibly the year after that. Snow geese (*Chen caerulescens*), for example, migrate in the thousands to breeding grounds in Alaska and northern Canada in the spring and summer. Once they have reproduced, they fly back south for more hospitable winter conditions. Next spring, they fly north to breed again. Figure 7.1E shows snow geese.

Many trees follow a pattern of annual reproduction, sustained over many seasons. Other trees reproduce less often than once a year. But in either case, the ability of some trees to survive through many rounds of reproduction is probably

greater than that of any other organisms. Bristlecone pines (*Pinus longaeva* and *P. aristata*) of the White Mountains of eastern California can survive thousands of years, continuing to reproduce century after century. Trees are

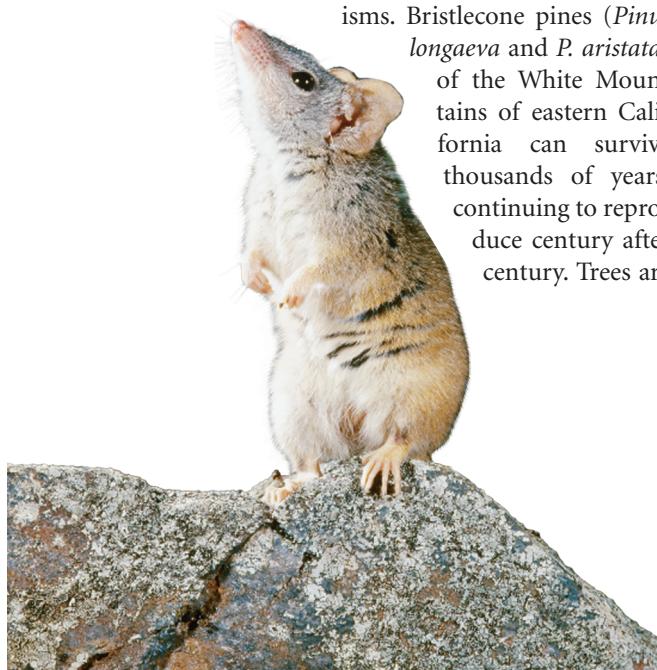


FIGURE 7.1D The Brown Antechinus

the silent witnesses of lives that are fleeting compared to theirs. Figure 7.1F shows bristlecone pines.

Some repeated reproducers show no annual cycle to their reproduction. Tropical species from plants to insects, like *Drosophila melanogaster*, are more likely to follow this pattern than temperate or arctic species. Humans are a tropical species in their evolutionary origins, and we reveal that in our continuing fertility throughout the year.

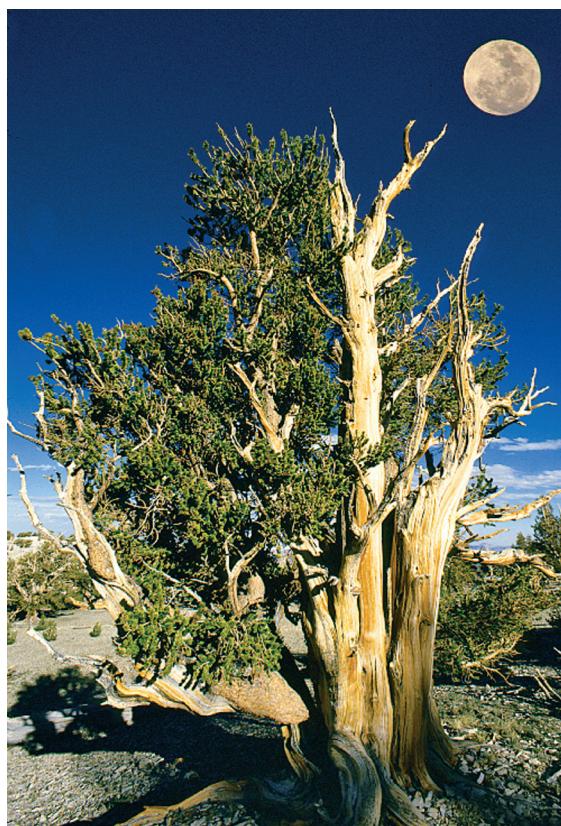


FIGURE 7.1F Bristlecone Pine

7.2 The fitness of semelparous organisms is the product of viability and fecundity

Some of the most spectacular “shows” in biology are put on by semelparous organisms—the animals and plants that reproduce a single time. Fields of grain that have grown abundantly suddenly set seed and then die. Mayflies emerge together on summer days, fill the skies with their mating swarm, lay their eggs, and then die in virtual unison, their myriad bodies clogging drains. (There are hundreds of species of mayfly, many of which have vestigial mouths as adults—guaranteeing an early death. A common American mayfly is *Dolonia americana*.)

Among vertebrates, one of the more dramatic semelparous life histories is that of Pacific salmon (genus *Onchorhynchus*). These salmon swim upstream from the ocean, overcoming waterfalls and hungry bears to find their way back to the small streams in which they were born. Schematics of semelparous life-history patterns are shown in Figure 7.2A.

For the scientist, the burst of reproduction that these species show is tremendously convenient. It makes the arithmetic of fitness simple, provided only that all adults are equally successful sexually. This means we assume that partners are so abundant during the brief burst of reproduction that we can assume that every female animal, or female flower, receives sperm or pollen. We also need to assume that all males are equally successful at fertilizing females.

If we make these assumptions, then the fitness of a semelparous organism is simply a product of its *viability* times its *fecundity*. **Viability** can be defined as the chance of surviving from the youngest juvenile stage to adulthood. **Fecundity** is the total output of successful gametes produced by an adult. As shown in Figure 7.2B, the Darwinian arithmetic of **fitness** in these life histories reduces to this product of viability (v) and fecundity (f), which is fitness (W):

$$W = v f$$

Semelparous life is like a pinball game with a single bumper that releases the balls for the next round of the game

when it is struck, and at the same time this strike terminates play, so that the parent ball rolls down to its death. 

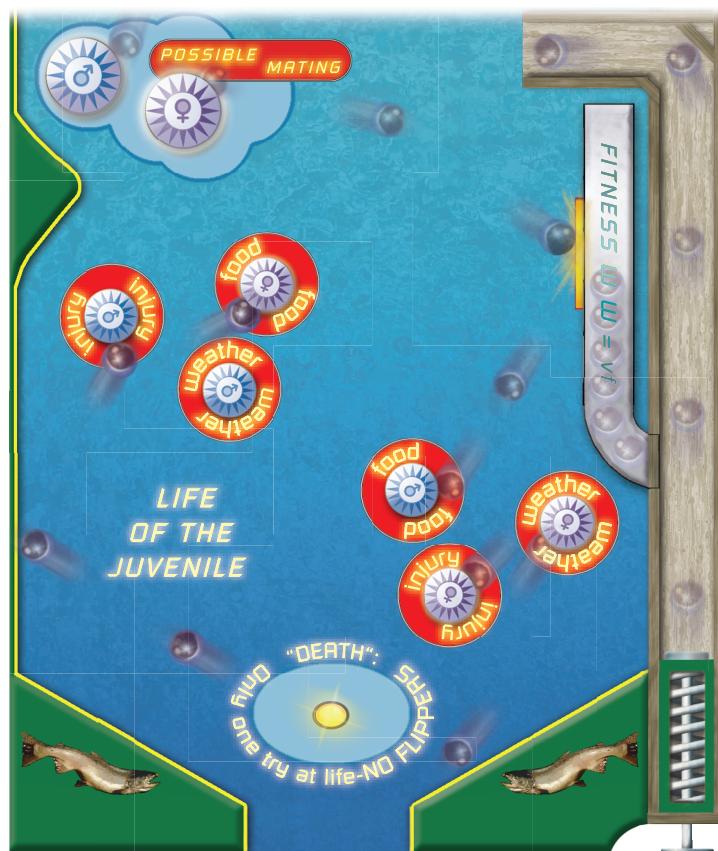


FIGURE 7.2B Pinball Structure of Semelparous Life Cycle This structure can be applied to most microbial life cycles, all monocarpic plants, univoltine insects, and many other kinds of organisms.

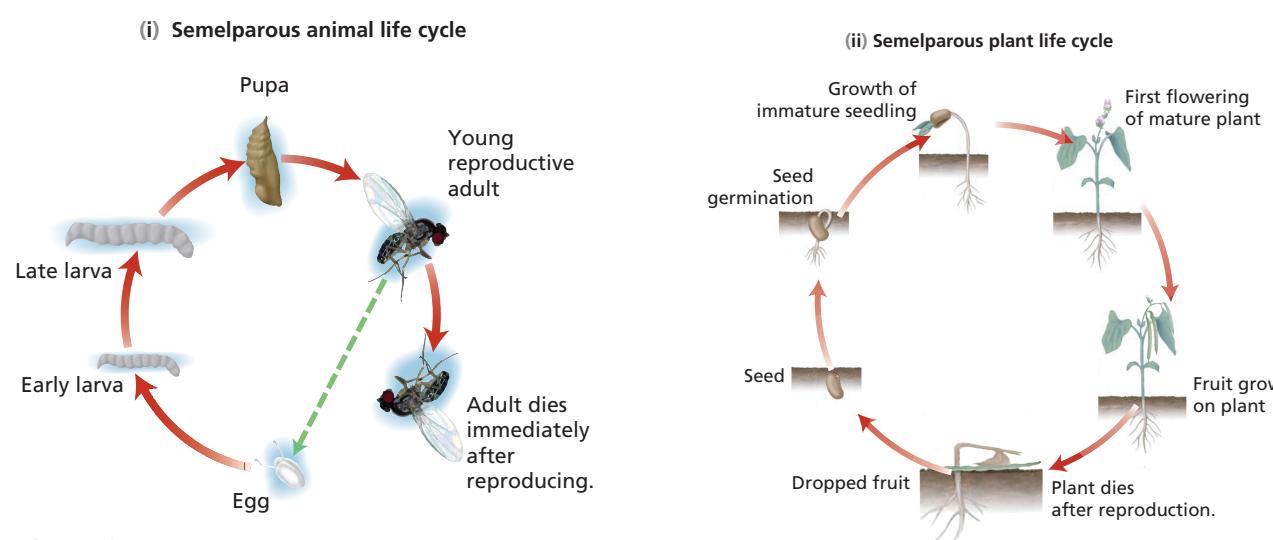
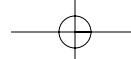


FIGURE 7.2A



Iteroparous organisms have age-structured life histories 7.3

The reproductive capability of an iteroparous organism generally changes with age. Thus an important aspect of a population of iteroparous organisms is its **age-structure**: the numbers and ages of all members of the population. To predict population growth in age-structured populations, we need to understand how patterns of survival and fertility vary with age.

To predict the growth of age-structured populations, we need some estimate of the fertility and survival of individuals as a function of age. Because the age of an individual is continuously changing, some convenient way of recording age must be established. We can usually accomplish this by creating discrete intervals, called **age classes**. All individuals in an age class are treated as equal. The limits of an age class are usually based on the properties of the organism and the amount of data that has been collected. For instance, in human populations, age classes are often broken down into five-year intervals. The first interval would be all individuals from birth to 4 years of age, the second age class individuals from 5 years to 9 years, and so on. This kind of analysis is shown in Figure 7.3A, for human demographic data. For an organism like a fruit fly, the age classes might be single days or two-day intervals. The chances of surviving—or the fertility of—a given age class is then based on the average of all members of the age class.

Age-specific probabilities of survival describe the chance that an individual in a certain age class will survive to become a member of the next age class. In females **age-specific fertility** refers to the number of offspring produced by a female in a particular age class that survives to become a member of the first age class. In males age-specific fertility is the count of offspring fathered by males of the age class.

Two basic techniques are commonly used to estimate age-specific fertility and **survival** probabilities. The most direct technique is to take a large group of identically aged individuals, or a **cohort**, and follow their survival and reproduction as they age. This technique is most easily used with laboratory or cultivated populations of animals and plants.

For some organisms that are very long-lived or that can't be subjected to experimental techniques, we need other methods. These other techniques involve looking at the numbers and ages of individuals in a particular population at a single point in time. After making several assumptions, we can estimate age-specific survival probabilities and fertilities. The product of this analysis is a **static life table**. The most obvious limitation of the ecologist's static life table is that the individuals used to construct it have not experienced the same environmental conditions. These environmental conditions can have a significant impact on current fertility or survival.

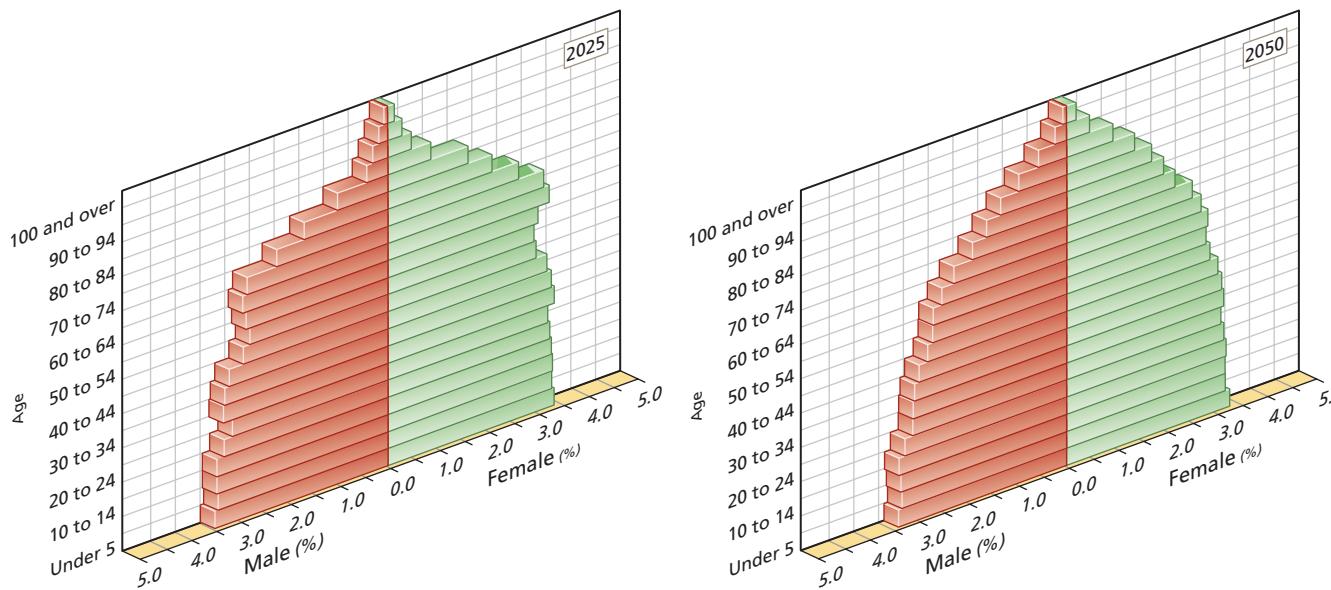


FIGURE 7.3A U.S. Age-Class Estimates for 2025 and 2050

7.4 Populations with age structure can grow exponentially according to a stable age-distribution

To follow the growth of age-structured populations, we require the fertility and survival probabilities of each age class. With this information, we can predict not only the total population size in the future but also the numbers of individuals in each of the age classes in the future. We will not go into the details of this process, but we will review the basic science of age-structured populations.

Suppose we have an organism with five age classes that we will call newborns, 1-year-olds, 2-year-olds, 3-year-olds, and 4-year-olds. Although the fertility of males could affect population growth, we assume, as is common, that they do not. We will further assume that the age-specific survival of males and females is the same. Table 7.4A summarizes the survival and fertility of the population as a **life table**.

No number is entered in the table for the survival of the 4-year-olds, because they are all presumed to die. If the population initially has 50 individuals in each age class, the growth of the total population and each age class is shown in Figure 7.4A. The total population size is simply the sum of each of the five

age classes. The behavior of the age classes over the first five or so years is variable from year to year. This variation reflects the oddities of the initial conditions. After some time we see that each age class starts to exhibit regular increases in size. In fact all age classes are increasing at the same rate, which in this example is about 4.7 percent per year.

When the different age classes begin to grow at the same exponential rate, as seen in Figure 7.4A, the different age classes will always make up a constant fraction of the total population. At this point we say the population has achieved a **stable age-distribution**. The population in Figure 7.4B has

TABLE 7.4A A Hypothetical Life Table		
Age Class	Female Fertility	Probability of Surviving
Newborns	0	0.8
1-year-olds	0.5	0.6
2-year-olds	1.2	0.5
3-year-olds	0.3	0.3
4-year-olds	0.02	—

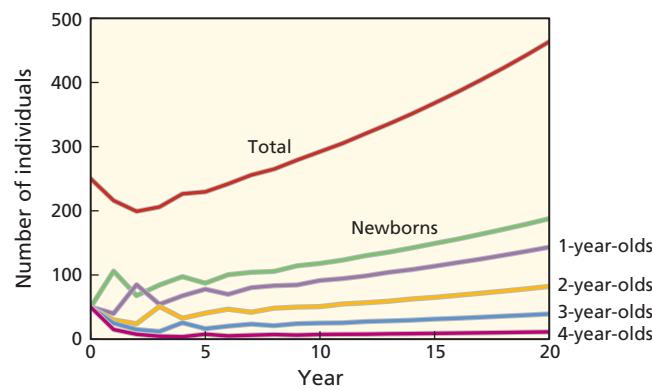
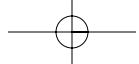


FIGURE 7.4A Population Growth in Age-Structured Populations
This population has five age classes, including newborns. The population starts with 50 in each age class. For the first 6 years, the age classes change haphazardly. After 10 years, each age class begins to increase steadily, as does the total population. At this point the total population and each age class are growing at the same exponential rate.





a stable age-distribution with newborns making up 40 percent of the population, 1-year-olds 31 percent, 2-year-olds 18 percent, 3-year-olds 9 percent, and 4-year-olds 2 percent. It is important to remember that even though a population is at a stable age-distribution, it may still be increasing in total size.

The shape of the stable age-distribution can give insights into the relative rate of population growth. In general, the proportion of individuals in the youngest age classes will be

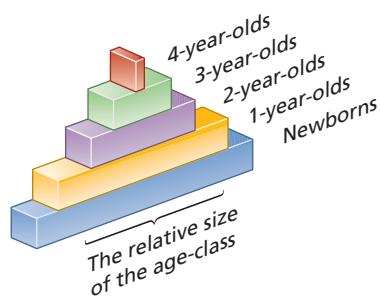


FIGURE 7.4B Population Growth in Age-Structured Populations

When all age classes are growing at the same exponential rate, the population is at a stable age-distribution. This means that each age class will occupy a constant percentage of the total population size. For the population in Figure 7.4A, the stable age-distribution is shown here. This type of display is called a population pyramid. The young age classes make up the largest fraction of the total population.

greater in faster-growing populations, such as the one in Figure 7.4C. This population has the same characteristics as the population in Figure 7.4B, except the fertility of 1-year-old females is 1.0 and the fertility of 2-year-old females is 2.0 (rather than the fertilities given in Table 7.4A). The resulting population is increasing by 26 percent each year (instead of 4.7 percent), and the fraction of the population in the youngest age classes is greater. 

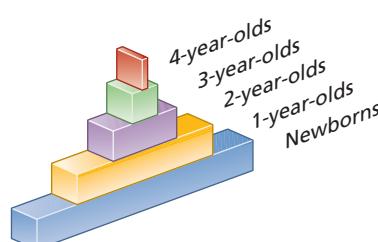


FIGURE 7.4C Population Growth in Age-Structured Populations

The relative proportions of individuals in each age class are affected by the rate of population growth. In slowly growing populations, the proportion of the population in the younger age classes is smaller than in rapidly growing populations. In Figure 7.4B, the population is increasing by 4.7 percent each year. In this figure, the population is growing by 26 percent each year.

Age Structure in Human Populations

The differences in age structure of rapidly and slowly growing populations are illustrated with human populations in Figure 7.4D. The rapidly growing Mexican population in 2000 has a sharply rising pyramid, while the more slowly growing U.S. population shows a more even distribution of people in the middle age ranges. Males and females are combined in these pyramids. Compared to the U.S. population, a much larger fraction of the Mexican population consists of very young individuals (less than 20 years old). Likewise, the U.S. population has a much larger fraction of people older than 80 years.

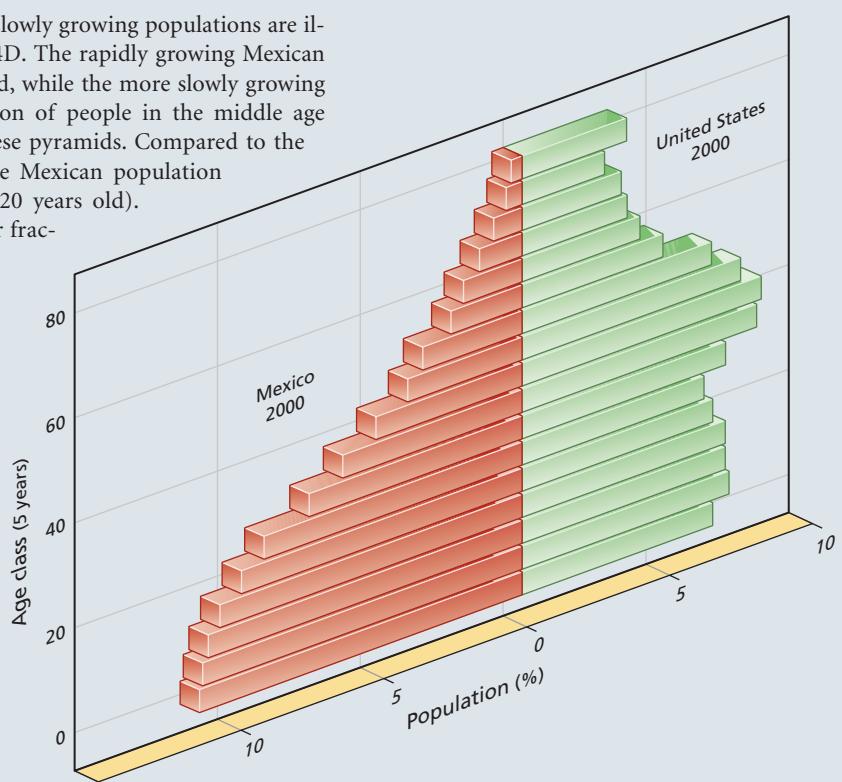
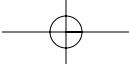
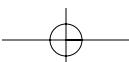
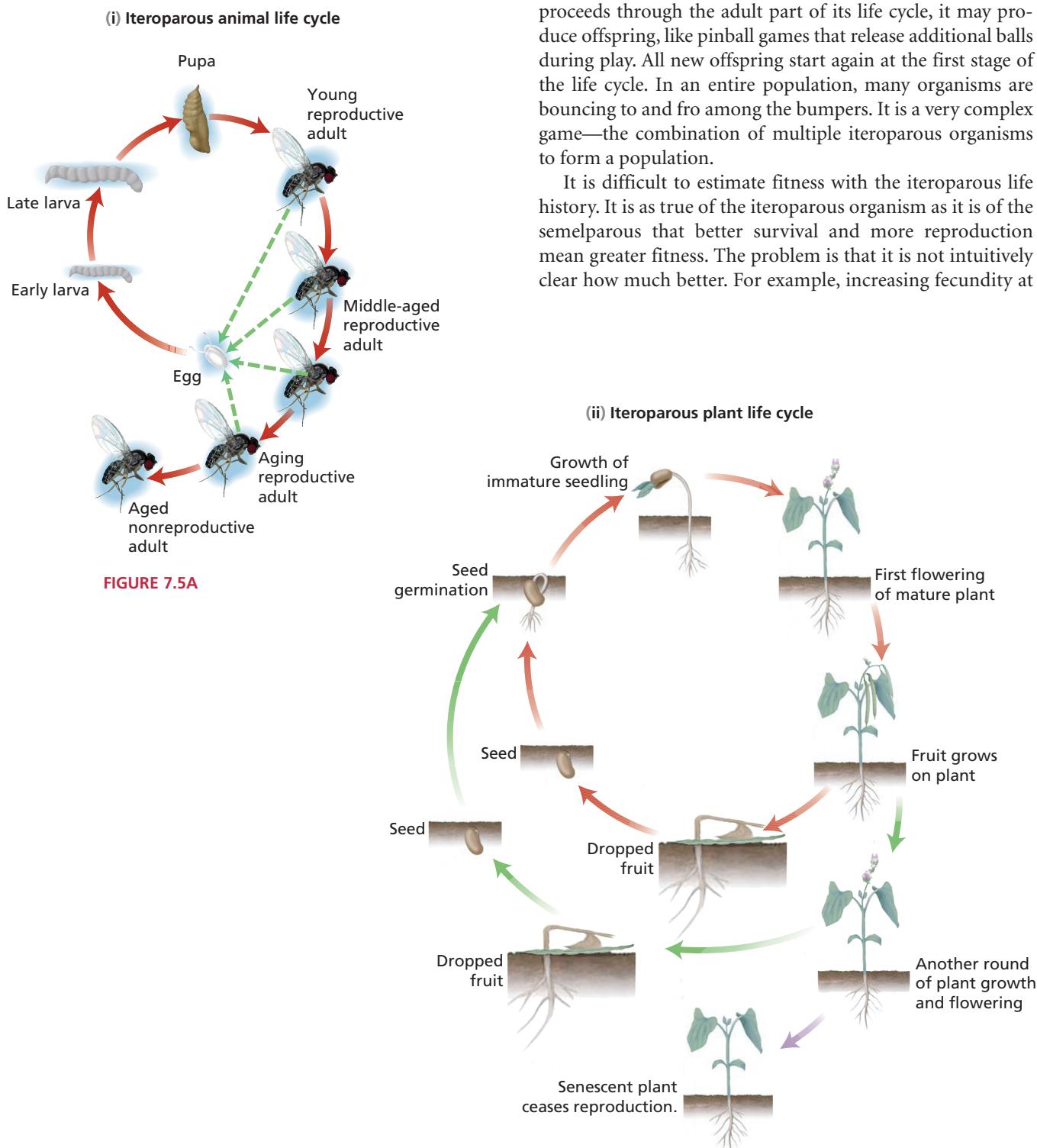


FIGURE 7.4D Age Structure of the U.S. and Mexican Populations in 2000



7.5 In iteroparous organisms, fitness can be calculated from estimates of population growth rates

Most iteroparous organisms are multicellular animals and plants. Their **life cycles** are sketched in Figure 7.5A. One way to think of these life cycles is that they are like semelparous life cycles, but with the first episode of reproduction repeated multiple times in the adults who survive to reproduce again.



any particular age should be a good thing for fitness; but there are reasons for supposing that increasing early fecundity would be better than increasing later fecundity. After all, in the wild, the organism might not survive long enough to reproduce at the later age, so any genetic capacity that it might have to reproduce then would be wasted.

This accounting problem in estimating fitness can be solved using the concept of population growth in age-structured populations. Repeated reproduction automatically makes populations age structured. The initial growth of an age-structured population is fairly chaotic, with the potential for large swings in the composition of the population—and thus large changes in repro-

ductive output. Over time, population growth tends to produce stable proportions of the different age groups, as explained earlier.

With stable proportions, the population size grows at a stable rate. This stable rate of population growth defines the fitness of the population. There are several different names for this fitness, including **intrinsic rate of increase** and the **Malthusian parameter**. It is usually represented by the lowercase letter r , although sometimes m or $\lambda = e^m$ is used, with m referring to Malthus. This definition of fitness is intuitively appealing because fitness is based on the idea of net reproduction, and net reproduction must determine the rate of growth in population size.

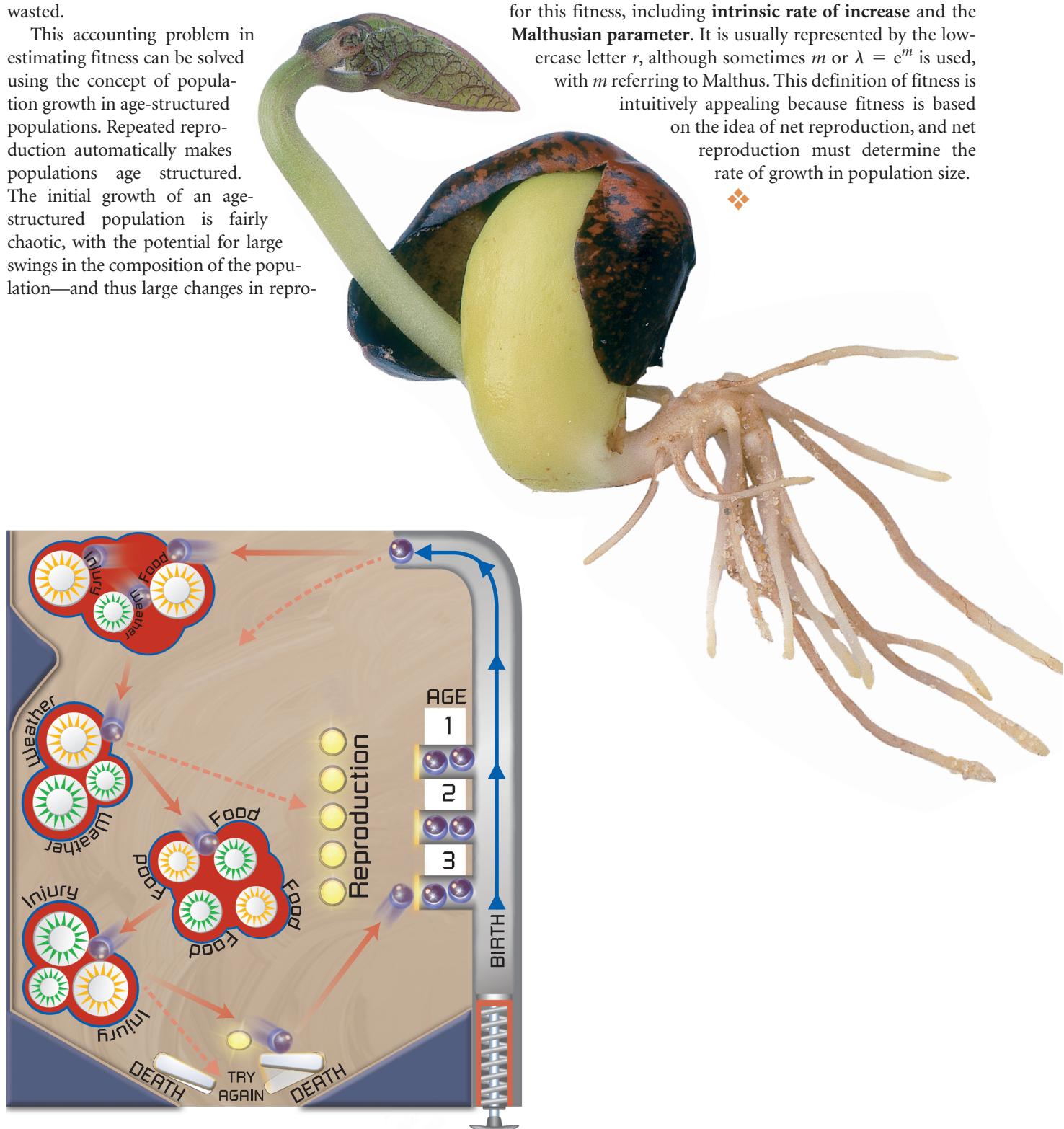
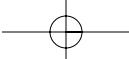


FIGURE 7.5B Structure of Iteroparous Life Cycle



7.6 A small increase in semelparous fecundity may be favored over iteroparity

An amazing fact about life histories is that semelparous animals and plants reproduce in a single burst, and then die. Why don't these organisms continue reproducing? Why does the Pacific salmon usually die right after spawning?

At one level, the answer appears to be that these organisms are killed by the act of reproduction. If the gonads of Pacific salmon are removed before spawning, they can live several years longer than intact, reproductive salmon; this is shown in Figure 7.6A. If the floral structures of a soybean plant are removed every time they grow, then the deflowered soybean plant can live much longer than an intact reproductive plant. Castrated *Antechinus* "mice" live months longer than intact "mice." For these organisms, and many like them, sex kills. Semelparous organisms do not go on reproducing, because they cannot. They are dead or dying.

But at the evolutionary level, this answer is not adequate. *Why don't semelparous organisms make some physiological investment in their continued survival?* This is called Cole's Paradox. The key must be reproduction, because the castration

experiments indicate that there is a **trade-off** between early reproduction and continued survival, as the Pacific salmon example shows. Semelparous animals and plants must be shifting resources to reproduction, away from their survival. The suspicion is that, in so doing, they increase their fitness—the product of viability and fertility.

We can calculate the conditions under which fitness is increased by shifting resources from later survival to earlier reproduction. One of the interesting special cases occurs when there is no juvenile or adult mortality. Under these implausible conditions, an increase of as little as one additional offspring during the first reproductive period is enough to make semelparity favored by natural selection over iteroparity. Even when there is significant mortality, semelparity may be favored by natural selection with just a small increase in fecundity during the first bout of reproduction. This quantitative comparison illustrates the extent to which natural selection is biased in favor of reproducing quickly, rather than waiting.

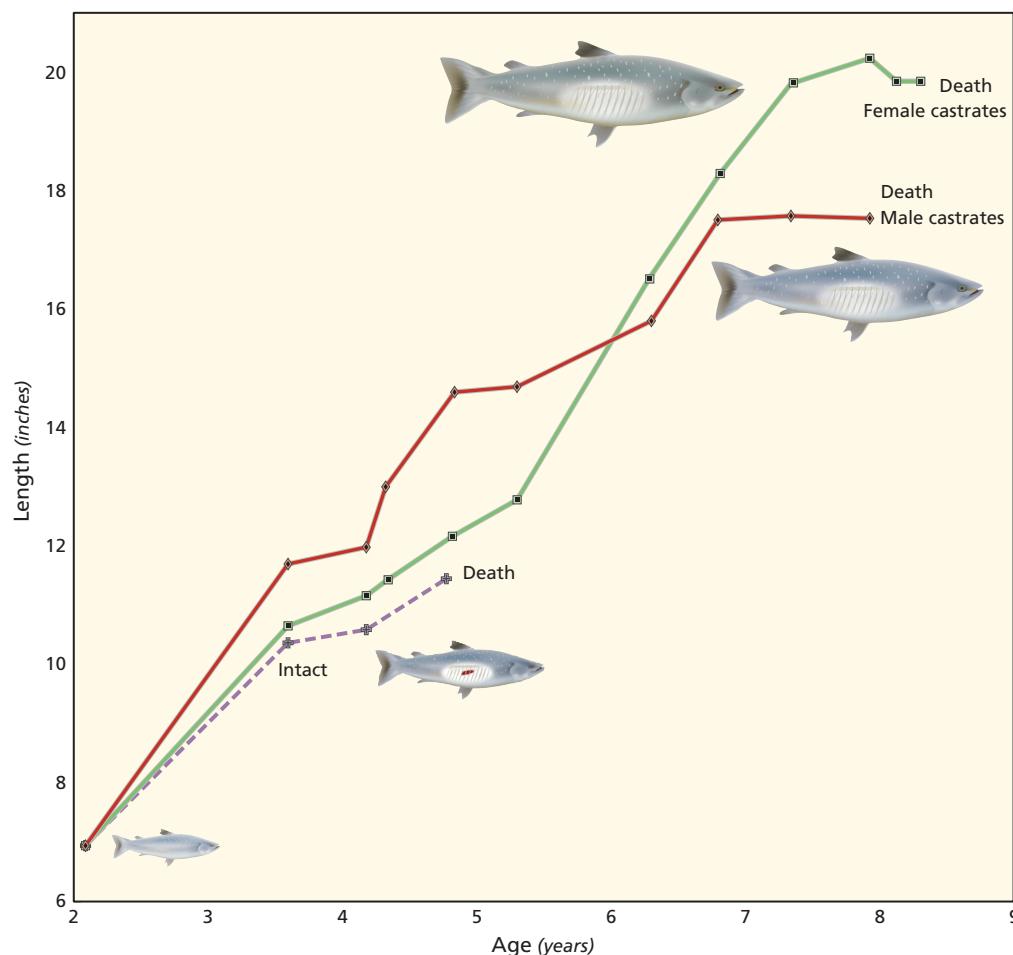
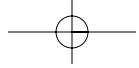


FIGURE 7.6A Pacific Salmon Castration Data Instead of dying within weeks, castrated Pacific salmon live for years. As the graph shows, castrated males and females go on growing for years after the intact fish have died. (From Robertson, 1961)



TRADE-OFFS IN LIFE-HISTORY EVOLUTION

When evolution increases one life-history character, another life-history character may decrease 7.7

Evolutionary costs or trade-offs arise when there are limits to the resources available to organisms—limits to the available food calories, water, amino acids, and so on. Organisms cannot solve their biological problems by getting more of such limited resources. A plant can synthesize only so much material from photosynthesis in a single day. An animal can feed only so much, so the amount of food energy available to fuel its metabolism must be limited. All of this can be summarized by stating that resources are limited.

Given that resources are limited, all organisms have the problem of what to do with them. For multicellular organisms, this problem is partly one of allocation of resources between reproduction and survival of the body. (Other allocation problems are discussed later.) This type of allocation in turn involves the flow of materials between organs. As shown in Figure 7.7A, a hypothetical fish example, the **cost of reproduction** often involves shunting materials to reproductive organs from the other tissues. Thus in the fish example shown, allocation will include the shunting of fats to gonads from the rest of the body. In the female gonad, fat can be used to provision eggs, increasing fecundity. In the male gonad, fat can be used to make more sperm. Or the fat can be retained in the rest of the body, where it can be used as a source of fuel for general metabolism, including the metabolism required for locomotion,

growth, and other functions. A growing organism, providing it survives, will later be able to build a bigger gonad. Resources devoted to reproduction and growth impinge on the animal's survival. The effect on life span of removing the gonads of Pacific salmon reveals this trade-off dramatically.

The evolutionary cost that is best established is the cost of reproduction. Much of the evidence for this cost comes from experiments or situations in which reproductive activity is increased, resulting in decreased survival; or in which reproduction is decreased, resulting in increased survival. We have already seen the example of Pacific salmon castration. A human example comes from institutionalized male patients with gross intellectual impairment. Some decades ago, a number of American male patients were castrated by their doctors. The castrated individuals lived longer than intact males did. Apparently, production of testosterone or related male behavior impairs survival in these institutionalized patients.

One of the best studies of this kind involved a fruit-fly species, *Drosophila subobscura*. J. Maynard Smith reduced the reproduction of female fruit flies by several different methods: maintaining some of them as virgins, sterilizing others by irradiation, and genetically eliminating the ovaries of others. As shown in Figure 7.7B, any manipulation that decreased fecundity increased adult female survival. ◆

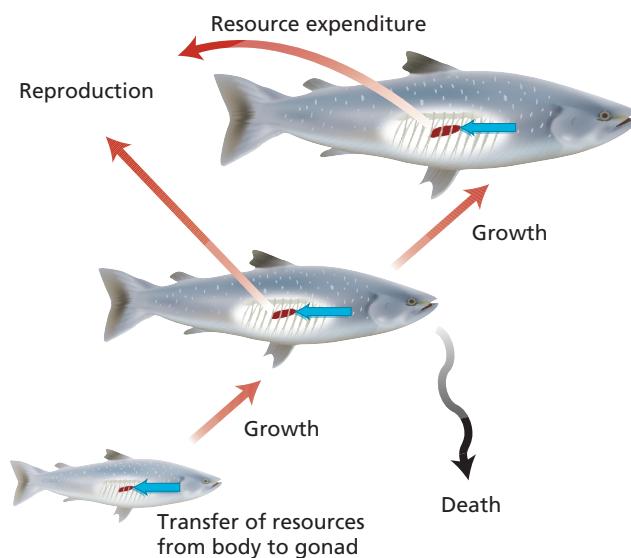


FIGURE 7.7A Shunting of Resources between Body and Gonad in a Growing Fish The growing fish faces trade-offs in its use of food energy. This energy can go to reproduction, growth, or survival. Growth may foster both survival and reproduction later in life.

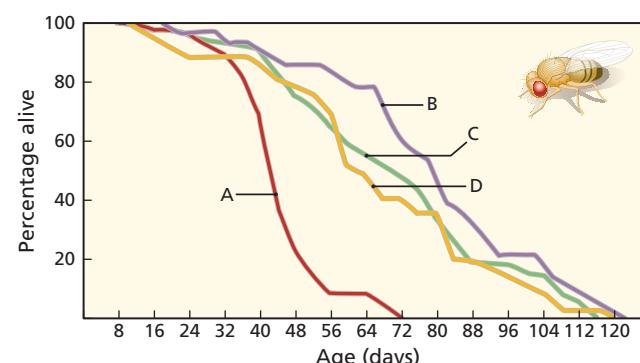
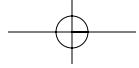


FIGURE 7.7B Effects of Mating and Reproduction on Survival in *Drosophila subobscura* A = normal mated females. B = females that lack ovaries and lay no eggs. C = virgin females, which may lay some eggs, but fewer than normal. D = mated females that have been sterilized by maintenance at high temperatures. The normal mated females lay more eggs and die sooner. (From Maynard Smith, 1958.)



7.8 Trade-offs between survival and reproduction may lead to the evolution of reproductive restraint

We will now consider the consequences of the cost of reproduction in more detail. When the cost of reproduction is considered theoretically, it is often found that natural selection favors producing an intermediate number of offspring. The logic behind this conclusion is shown in the box, shown below. Total fecundity rises with the number of offspring, because that is what fecundity means. If there is a trade-off between parental fecundity and parental survival, the survival of the parent will fall as fecundity increases. If we use net fecundity as a measure of fitness per reproductive season, the curve relating total fecundity to the number of offspring produced in each season of reproduction is humped. If no offspring are produced, individual fitness is zero. If many eggs are laid, the parent will quickly die—approximating the semelparous pattern of reproduction. Somewhere in the middle may be the right fecundity per round of reproduction, the seasonal fecundity at which fitness over the whole life is at a peak.

The best-studied examples of this pattern are in nesting birds, because experimenters can easily add or subtract eggs

from the nest, as noted earlier. Figure 7.8D shows the data from a study of this kind using great tits (*Parus major*). Great tits usually lay an intermediate number of eggs—about eight. If adults are given additional eggs to rear, they almost always succeed in rearing the young to fledging. Why don't they lay more eggs each year? The data of Figure 7.8D reveal that adults laying more eggs have lower survival rates. These findings were obtained in natural breeding populations, so they demonstrate well what evolution actually does. Faced with a trade-off between fecundity and survival, evolution compromises, leading to the evolution of reproductive restraint.

Note that in some cases evolution will not compromise. In the case of semelparous organisms, evolution pushes reproduction to its maximum value, effectively killing the parent. Natural selection is always focused on fitness, and thus on reproduction. For this reason, survival must ultimately lose out against reproduction, when there is a trade-off. We live only in order to reproduce.



Selection Favors an Intermediate Number of Offspring

The figures show the situation birds face within a breeding season. This is like semelparous breeding. As an evolutionary problem, fitness for the breeding season is maximized using the product of fertility and viability, the net number of offspring reared.

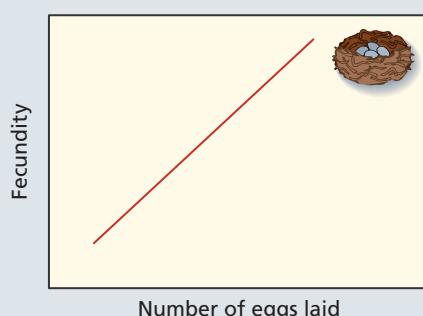


FIGURE 7.8A

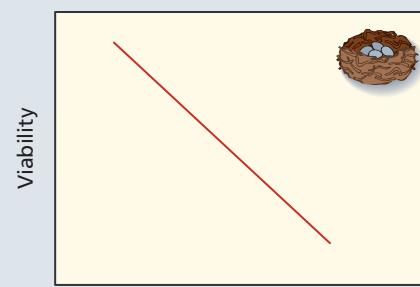


FIGURE 7.8B

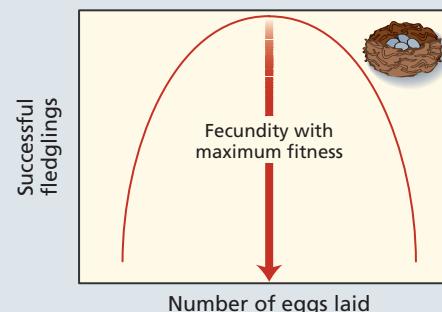
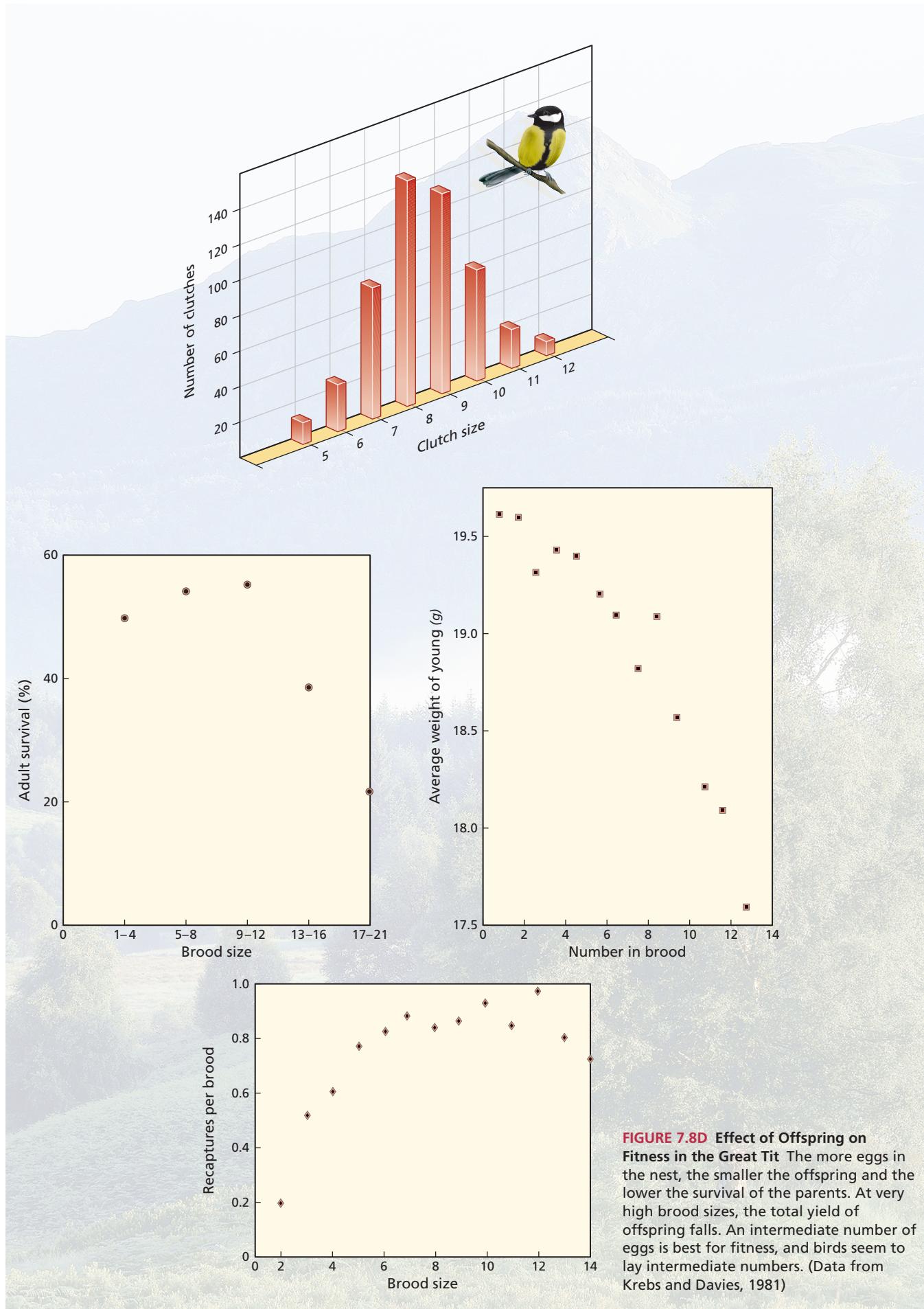
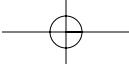


FIGURE 7.8C





7.9 Trade-offs between offspring size and offspring survival lead to the evolution of intermediate size

The cost of reproduction is not the only trade-off that shapes the evolution of life history. Another trade-off occurs between the viability of the offspring and the number of those offspring. A particularly important factor that tends to produce this trade-off is size. In most organisms, larger offspring tend to survive better than smaller ones. Sometimes this size factor involves the caloric reserves available to the offspring. Bigger babies usually have more fat. Sometimes, as in fish, the size factor involves size-dependent predation. When you are a small fish, there are more fish that can eat you. Whatever the reason, bigger is usually better in most species. (An exception would be larger babies in humans, which had higher infant death rates in the era before routine Cesarian sections during delivery.)

But if larger offspring do better, it is easier for virtually all parents to produce more offspring when the offspring are smaller than when they are larger. And natural selection favors the production of more offspring, within the limits of their cost in reduced adult survival, as we have seen. Therefore, we have a classic

trade-off situation. As shown in the box, we expect that the fitness of the parent will often be greatest at an intermediate offspring size. (For the offspring, their individual fitness will usually be greater if they are larger, because both viability and fecundity will usually benefit from increased size.)

Figure 7.9A shows the results from a study of the evolution of offspring size in the lizard *Uta stansburiana* from the coastal ranges of California. In female offspring from the first bout of reproduction, the data indicate that the optimal egg size is about 0.5 grams. The actual egg size turns out to average about 0.4 grams. The reason for this disparity is an additional constraint on the evolution of egg size. Larger eggs tend to become stuck in the mother's body, leading to reproductive failure. Therefore, selection favors an additional reduction in egg size below that which is calculated as optimal based on the relationship between egg survival and its size. This is a case in which there are multiple trade-offs between life-cycle stages, in this instance between parent and offspring.

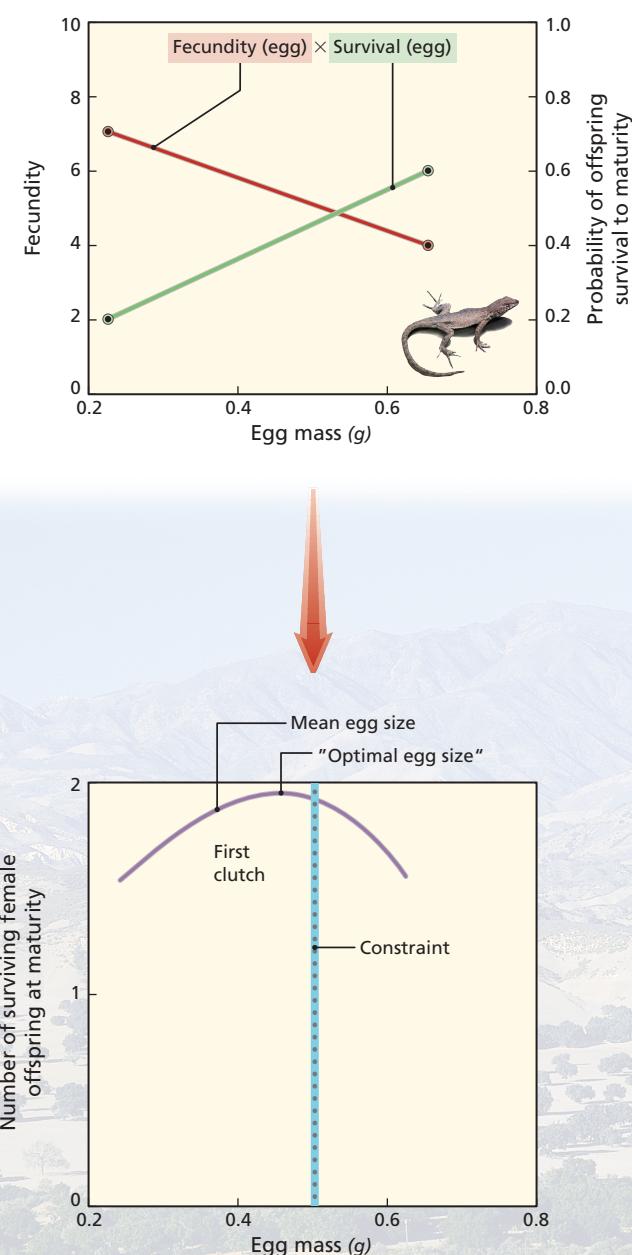
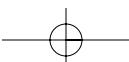
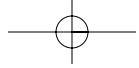


FIGURE 7.9A A Trade-Off between Egg Size and Egg Number in a Lizard (*Uta stansburiana*) from Coastal California Females that lay small eggs can lay more of them. But larger offspring survive better, except for really large eggs, which become stuck inside the mother.





Evolution of Offspring Size

The larger each offspring is, the fewer a typical parent can produce.

Offspring that are too small die off. But once the offspring are large enough, they get no additional benefit from being larger.

Calculating the effect on parental fitness of offspring size gives an intermediate peak.

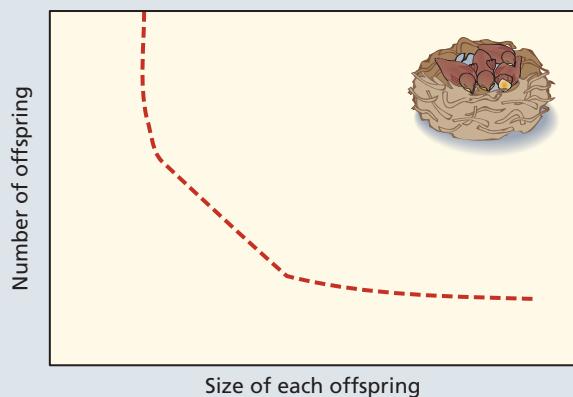


FIGURE 7.9B

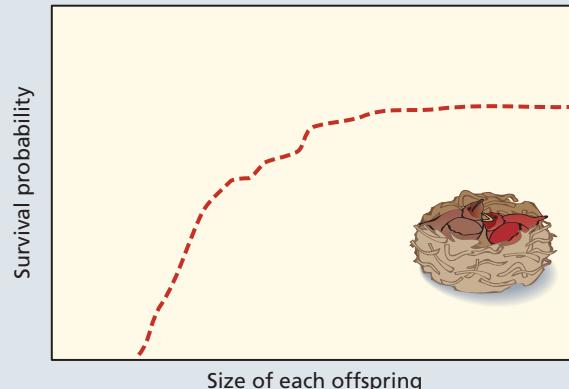


FIGURE 7.9C

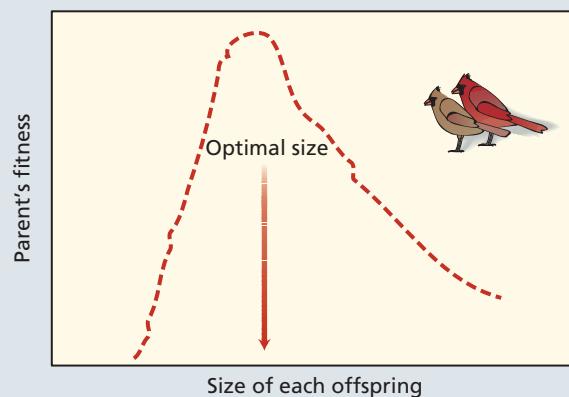
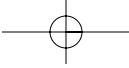


FIGURE 7.9D





EVOLUTION OF AGING

7.10 Aging has been studied from very different perspectives, including evolutionary biology

The broad features of aging are known to all of us. In humans, **aging** begins as minor impairments between the ages of 30 and 50: gray hair, hair loss, reduced sexual performance, loss of muscle tone, unreliable memory, and so on. Figure 7.10A shows something of the overall progression during aging, in a composite photo of a boy, young man, middle-aged man, and old man. After the age of 50, as shown in Figure 7.10B, the impact of aging becomes altogether more profound. Almost all degenerative disorders increase in frequency. Cardiovascular disease becomes rampant. Strokes and cancer kill many. In total, death rates rise exponentially until the age of 90. Together with death, general impairment increases progressively. All types of work, sport, and play become harder, if not impossible. Each of the organs, the brain among them, is less able to perform its functions. This is a spectacle of pervasive deterioration—unrelenting, even accelerating.

The puzzle of aging has interested biologists and medical doctors for thousands of years. Ancient Egyptians developed a cult of immortality; much of their culture centered on cheating death, including their practice of mummification. Aristotle wrote a short book about aging. The Chinese **Taoists** built much of their religion around the explanation and control of aging (Figure 7.10C). In Renaissance Europe, such luminaries as **Sir Francis Bacon** worked on aging as a research problem. In modern times, the National Institute on Aging has given millions of dollars to cell biologists who propose to solve the problem using techniques of molecular biology.

Aging is both easy and difficult to study. It is easy to document the changes that occur in organisms during aging, with

one exception: It is very difficult to study organisms that live a long time. Animals like elephants are often considered long-lived; and they are, if we compare them to most other animals. But the really long-lived organisms are trees, shrubs, and grasses. Individual trees, particularly the bristlecone pines mentioned earlier, can live thousands of years. Some biologists doubt that such organisms age at all. However, it is hard to have a very strong opinion, simply because we study too small a fraction of their lives. We just don't know. Meanwhile, it is probably more appropriate to confine scientific attention to aging in organisms that biologists can study as a practical matter.

In such organisms, the biology of aging is quite clear. As chronological age increases, well-studied plants and animals tend to suffer pervasive deterioration across the full range of functions and tissues. It is difficult to find organisms that improve biologically with adult age. In humans and rodents, in particular, we have amassed a large amount of data on aging, from the level of biochemistry to that of cognitive function. None of it is encouraging.

In researching many biological processes, it is common to study mutants or manipulated organisms in which the process is stopped. For example, we study vision in fruit flies by using mutants that are blind. The problem with the study of aging is that we cannot create organisms that stop aging completely. Instead, some scientists study aging in organisms that die sooner rather than later. This creates quite a few problems, because dying sooner can occur via many physiological processes that have nothing to do with normal aging. For a lot of organisms, accidents—such as being stepped on—end life sooner. In aging research, it is more appropriate to test for interventions in which life



FIGURE 7.10A The Aging of the Human Male

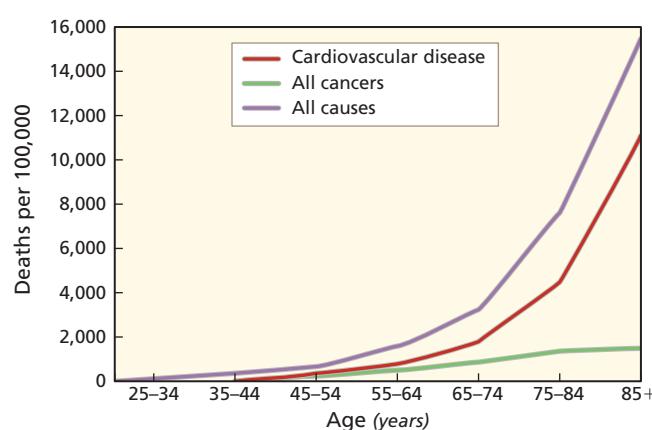


FIGURE 7.10B Different Causes of Death as a Function of Age

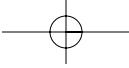


FIGURE 7.10C Painting of a Taoist Rite for Achieving Physical Immortality

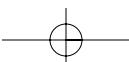
span is increased, because normal aging processes must somehow be alleviated in such longer-lived organisms.

Evolutionary biology has developed a program for the study of the biological aging of whole organisms. The foundation of this program is an evolutionary theory that explains aging based on a decline in the force of natural selection, which we explain in more detail shortly. Using this evolutionary approach, it has been possible to postpone aging in experimental organisms, such as fruit flies and mice. Progress has also been made on the genetics of aging, particularly in nematodes and fruit flies.

Between genetics and evolutionary biology, a lot of headway has been made in research on aging. The evolutionary



research is outlined in the remainder of this chapter, in the following sequence. First, we describe aging as a life-history phenomenon. Then we introduce the basic theory underlying the evolutionary biology of aging. This theory leads immediately to a general and important prediction about the occurrence of aging in nature, especially the situations in which it should always occur and those in which it should never occur. We end this chapter by discussing the core of the research program, which consists of experiments in which evolutionary principles are used to substantially postpone aging.



7.11 The survival and fertility of iteroparous plants and animals change with age

In many natural populations, death is often due to environmental factors such as disease, predation, and accidents. However, if a population is largely shielded from these factors, a process called senescence will gradually accelerate mortality and decrease fertility with age. **Senescence** is the gradual breaking down with age of the physiological machinery, and the subsequent increase in rates of mortality.

The effects of age on survival and fertility can be studied in **cohorts**, or groups of identically aged individuals. Typically, a fixed number of young individuals are followed until all have died. At regular intervals, researchers record the number alive and the number of offspring produced by members of the cohort. This life-table information can then be used to estimate age-specific mortality and fertility as in Table 7.4A.

Figure 7.11A, part (i), shows age-specific mortality in fruit flies. Initially there is a dramatic increase in mortality at

young ages (5–20 days). However, at approximately 20 days of adult life, the mortality rates reach a plateau. These data were collected for a large cohort (~10,000 individuals of each sex). The mortality rates in the plateau apply only to 1 percent or less of the cohort of flies. This plateau has been seen in many other organisms, including humans. It is likely that the same evolutionary forces that lead to aging are also responsible for these plateaus.

The fertility of males and females also declines with age, as shown in part (ii) of Figure 7.11A. Some organisms do not reach peak fertility immediately after they reach sexual maturity, as with the herb, *Phlox drummondii* (Figures 7.11B and 7.11C).

It is possible for individual organisms to survive past the age when they last reproduce. Today this happens quite often with human females, for instance. Is there an evolutionary advantage to living past reproductive age? For many species, the answer is no. However, for some species, mostly vertebrates, post-reproductive individuals may still take part in the care of offspring and thus contribute to their fitness.

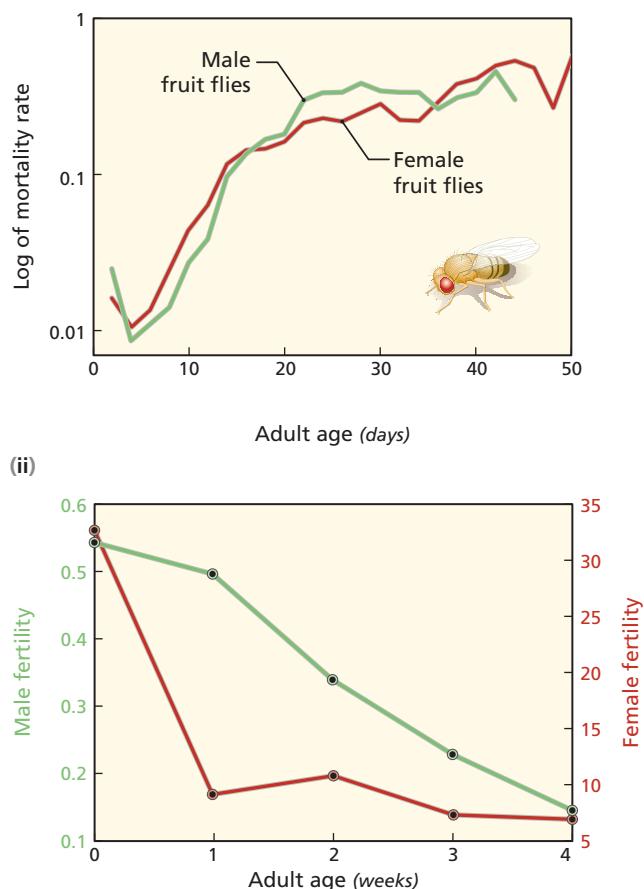


FIGURE 7.11A In fruit flies, mortality increases in a linear fashion on a log scale, until late in life, where a plateau occurs. Female fecundity is the number of eggs laid. In males, fertility can be measured by giving males multiple females and seeing how many are fertilized. Both fecundity and fertility decline with age in both sexes.

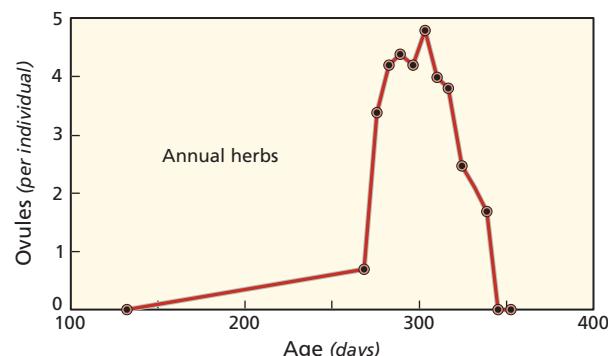


FIGURE 7.11B Fecundity in *Phlox drummondii* Plants exhibit the same general trends in survival and fertility as do animals.



FIGURE 7.11C In this plant, *Phlox drummondii*, each flower produces three ovules; usually, every ovule becomes a seed.

Humans follow these same general patterns (Figure 7.11D). Between 1994 and 2000, females aged 25–29 years produced the most offspring per 1000 females. In the United States the delay in peak female fertility is affected by factors like schooling, starting careers, and other considerations that influence individual decisions to have children. Although these factors also influence to some extent the very low fertility of women aged 40–44 years, physiological infertility is also a significant factor at these ages.

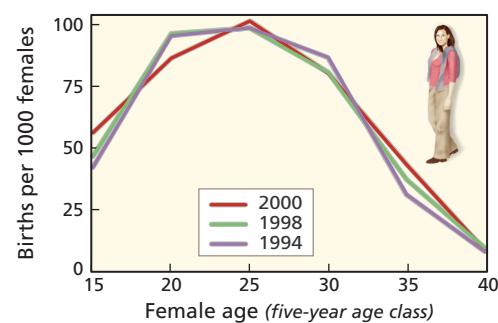


FIGURE 7.11D Age-Specific Fertility of U.S. Females



7.12 The force of natural selection acting on survival falls with adult age

The core idea of modern evolutionary theories of aging is the decline in the force of natural selection with age. This is not an assumption or a speculation. It is instead a result that has been derived mathematically from the first principle of an age-structured population, as defined at the start of the chapter. Therefore, we know that the **force of natural selection** acting on a fixed percentage change in age-specific survival has a declining effect after the start of reproduction in age-structured populations.

The force of natural selection depends on the age of an organism, as shown in Figure 7.12A. Before the start of reproduction, the force is at 100 percent. Natural selection is very strong. One way to understand this is to think about a dominant gene that kills every individual carrying it. These genes are known in humans, fruit flies, nematodes, and other or-

ganisms. But death must come at a particular age. Suppose that it comes before reproduction, before the age b . When it does, then that gene kills itself off. It will never be transmitted into the next generation. Natural selection has completely eliminated it, thanks to its 100 percent strength.

Now consider the period after the last reproduction, at age d . After d , a lethal gene has no effect on its own reproduction, because its carrier could have already produced offspring. Thus very bad genetic effects become neutral for natural selection, so long as they occur at late enough ages.

Between the start and end of reproduction in the population as a whole (ages b and d), the force of natural selection progressively falls because less and less reproduction occurs at ages after the lethal gene takes effect. With partially deleterious genes, the effect is not as dramatic, but it is qualitatively the same—initial strong natural selection, selection falling in strength during the period when reproduction occurs, and finally an absence of effective natural selection after the end of reproduction.

With natural selection as the ultimate source of most adaptation, this pattern of natural selection as a function of age is expected to produce health during youth and decrepitude at later ages—in a word, aging.

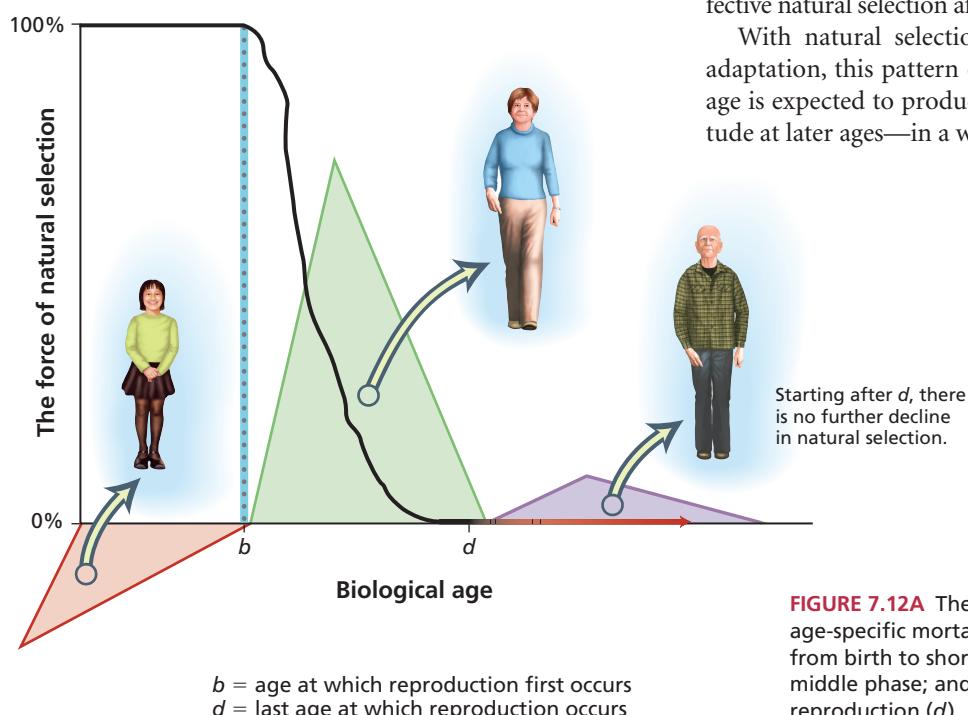


FIGURE 7.12A The force of natural selection acting on age-specific mortality has three phases: (1) Childhood, from birth to shortly after maturation (b); (2) aging, the middle phase; and (3) late life, after the end of reproduction (d).

The Aging of Fertility

Fertility ages, too: All organisms from normal age-structured populations that have been followed carefully in the laboratory eventually become less fertile. It turns out that the force of natural selection acting on fertility also eventually declines with age. However, it does not necessarily decline from the start of adulthood. It can even increase into middle age. This may be part of the explanation for the greatly increasing fertility of some fish and trees during their adult period.

A key feature of the evolution of declining fertility in late life is that it is not a mere by-product of the same evolutionary or physiological processes that produce declining survival. There is a sepa-

rate evolutionary pattern that leads to the reduction in fertility. Anatomically and physiologically, this disparity helps explain the aging of fertility when the reproductive organs are relatively autonomous from the rest of the body. In many organisms, insects being one example, somatic cells no longer divide during adulthood; yet germline cells continue to replicate. This may explain the lack of synchrony between reproductive aging and the aging of the rest of the body. This lack of synchrony is obvious in the case of human menopause, but many females in a variety of mammalian species lose fertility long before the rest of their body dies of aging.

Aging should not evolve in fissile organisms, but it should 7.13 in life cycles without vegetative reproduction

An important feature of the evolution of aging is the difference between populations that are expected to age and those that are expected not to age. The critical factor is the nature of reproduction as shown in Figure 7.13A.

Some organisms **reproduce vegetatively**. Part of the organism breaks off, and then both parts develop independent lives. This is common among trees, shrubs, and other plants. It is not as common among multicellular animals, except for the Cnidarians (corals, hydras, sea anemones). Some hydras are shown in Figure 7.13B. *Hydra* species often reproduce by budding a new hydra from their bodies. In tubular sea anemones, some species reproduce only by splitting in two, the two half “tubes” then closing in to form a functionally complete anemone, a process called **fission**. When the mortality rates of budding hydra and splitting anemone species are carefully monitored in the laboratory, they do not increase with age. These species are essentially free of aging. The reason is that these organisms never become adults. The single reproductive act creates two juveniles, so there is no adult to age. If aging were to occur in such organisms, it would lead to the deterioration of the offspring from fission. But since that is the only way reproduction occurs, all members of the population would progressively deteriorate. This universal deterioration would result in the extinction of the population. Therefore, with fissile reproduction, aging does not evolve.

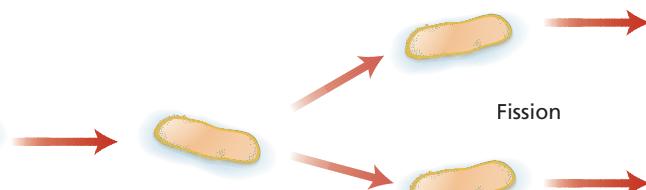
The other extreme includes organisms that reproduce only by eggs or ovules (see Figure 7.13A). Most multicellular organisms reproduce this way—vertebrates, insects, mollusks, most flowering plants, and so on. In all these species, the requirements of the conventional evolutionary theory of aging are met. Aging is the firm expectation.

Some biologists don't think that fish age. However, the fish that they refer to are those that are hard to study, such as long-lived rockfish species. Fish that are studied for their entire lifetimes in the laboratory are always found to age. In general, there are no examples in which nonvegetative species have been shown to be free of aging. The non-aging vertebrate is a myth, even though an attractive one.

Besides the immortal and the mortal organisms, there are some species that can

reproduce both vegetatively and sexually. These ambiguous organisms include coral and many plant species. For ambiguous organisms, there are no general predictions; they may or may not age.

(i) Immortal or non-aging organisms



(ii) Mortal or aging organisms

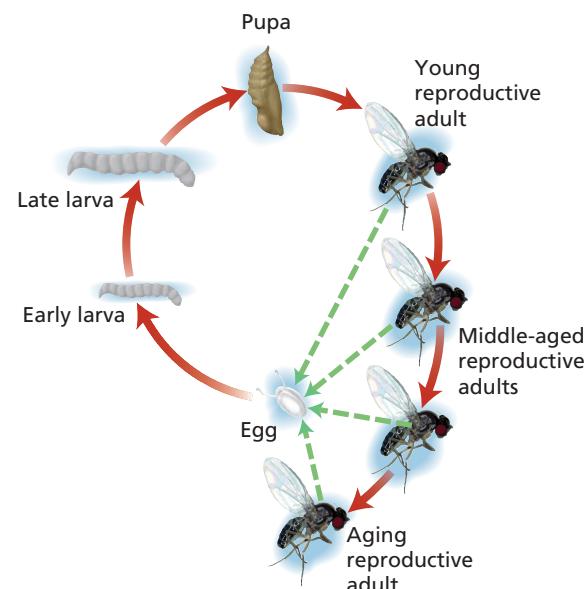


FIGURE 7.13A Two Types of Organisms (i) Immortal, or non-aging, organisms include, for example, bacteria, many protozoans, and some coelenterates, all with fissile or fragmenting reproduction. (ii) Mortal, or aging, organisms include plants and animals that reproduce only by means of eggs or seeds.



FIGURE 7.13B *Hydra*, a Small Aquatic Invertebrate Animal

7.14 Changing the force of natural selection can produce rapid evolution of aging patterns

The idea of the evolution of aging leaves the impression that aging can be changed only with difficulty, over long periods of evolutionary time. This impression is erroneous. Evolution can change aging patterns very quickly.

This rapid evolution has been shown with fruit flies. The experimental trick involved is to change the first age of reproduction. As we noted earlier, the force of natural selection on survival starts to decline once the population begins to reproduce. In fruit flies, it is easy to change the age of first reproduction experimentally simply by discarding all eggs laid before the preferred age of reproduction. Normally adult fruit flies are kept until the age of 14 days, made to lay eggs, and then discarded. But the adult flies can be kept for a longer period as shown in Figure 7.14A. This regimen changes the

force of natural selection by increasing it at later ages. If aging is controlled by natural selection, then this change should produce large changes in mortality patterns, if evolution is given several generations over which to act. As shown in Figure 7.14B, this is in fact what happens: Delayed first reproduction leads to increased survival at later ages within 10–20 generations.

The flies that live longer in these experiments have evolved extensive physiological changes over the course of more than 100 generations of additional selection. They resist stress better. They can fly longer than other flies. They are able to have sex at later ages. The females are more fecund when older. These are not organisms that simply endure decay for a longer period; they are more vigorous at later and middle ages, long after most normal flies are dead. Physiologically, these flies do not prolong aging, they prolong active life.

These experiments have shown that aging is eminently controllable using evolutionary tools. They do not, however, suggest that humans should be selected for delayed aging. Progress with human aging cannot wait the hundreds of years that human breeding would take, if we were to follow the evolutionary pattern of the late-breeding fruit flies. ♦

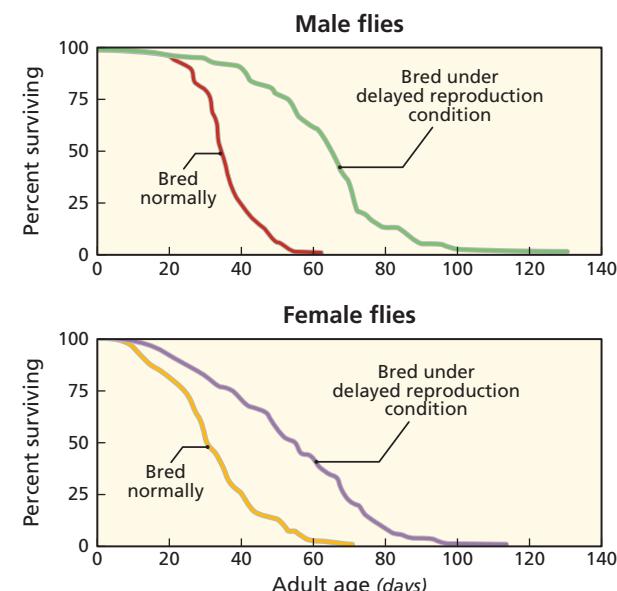
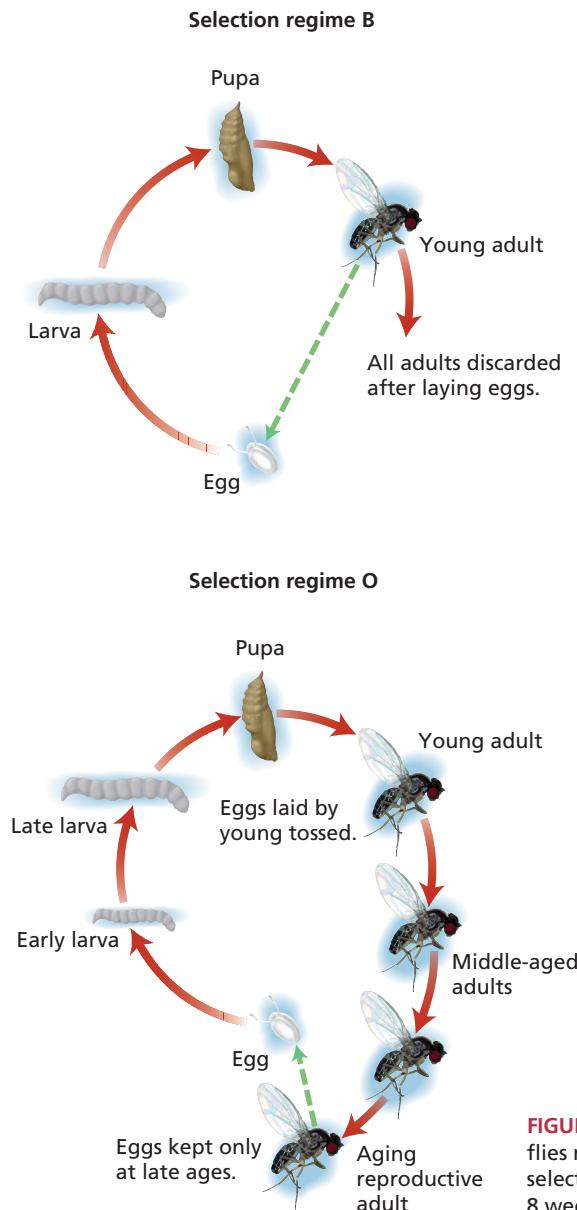


FIGURE 7.14B The evolution of postponed or slowed aging in fruit flies arises from delayed reproduction.

FIGURE 7.14A Lab Evolution of Aging in Fruit Flies (i) In the B regime, lab fruit flies reproduce in the first few days of adult life. (ii) In the O regime, natural selection is prolonged by delaying female reproduction until adults are at least 8 weeks old.

SUMMARY

1. Life history is the central clearing ground of evolution, ecology, and organismal biology. The life history determines fitness, the central parameter of evolution. The life history sums up all the ecological forces that shape an organism's way of life in its environment. The life history also makes manifest the organism's multiple adaptations, the articulation of anatomy and physiology that defines the potentialities and limits of that organism.
2. A basic problem of life history is the arithmetic required to proceed from life history to fitness. In semelparous organisms this arithmetic is relatively simple, when there are no complications due to mating. Under such conditions, the fitness of a semelparous organism is the product of viability and fertility. But many plants and animals reproduce multiple times over their adult life span. These species have age-structured populations. Age-structured populations require different models. Specifically, we need to know the age-specific fertilities and the age-specific survival of individuals. Age-structured populations grow exponentially at a constant rate after they have reached their stable age-distribution, in theory. In these iteroparous organisms, the arithmetic of fitness is far more complex. However, in populations that have stable age-structure, fitness is given by the growth rate of the population.
3. Trade-offs arise when one part of the life history has a functional antagonism with another part of the life history. The best-known trade-off is that between reproduction and adult survival. Reproducing more tends to result in earlier death among the adults of many species, whether that increased reproduction occurs because of genetic, anatomical, physiological, or behavioral manipulation. This cost of reproduction sometimes leads to the evolution of restrained reproduction. There are other life-history trade-offs, including those between fecundity, offspring size, offspring viability, and growth.
4. Aging is not universal. It occurs in nonfissile organisms because the force of natural selection on survival falls with adult age. In fissile organisms, like many Cnidarian and plant species, the force of natural selection does not fall, and aging does not evolve. Patterns of aging are readily shaped evolutionarily by manipulating the force of natural selection, which is itself easy to manipulate by changing the age of first reproduction.

REVIEW QUESTIONS

1. List some life-history characters, and define each one.
2. In semelparous organisms, which two variables define fitness?
3. What kind of semelparous animals are univoltine?
4. If an animal or plant reproduces by fission, can it be iteroparous?
5. List some life-history trade-offs or costs, and define each one.
6. How is it possible to make inferences about the cost of reproduction from manipulating the number of eggs in bird nests?
7. What is the effect of delaying the onset of a population's reproduction for many generations?
8. What do you predict will be the effect on early fertility of delaying the start of reproduction for many generations?

KEY TERMS

age-class	Cole's paradox	iteroparous	survival
age-specific fertility	cost of reproduction	life cycle	Taoist
age-specific probabilities of survival	fecundity	life history	trade-off
age structure	fertility	life table	univoltine
aging	fission	Malthusian parameter	vegetative reproduction
Bacon, Sir Francis	fitness	semelparous	viability
cohort	force of natural selection	senescence	
	intrinsic rate of increase	stable age-distribution	

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