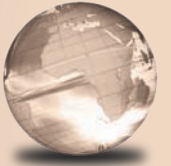


GLOBAL
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Elements of ECOLOGY

NINTH EDITION

Thomas M. Smith • Robert Leo Smith

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Ecology

Ninth Edition
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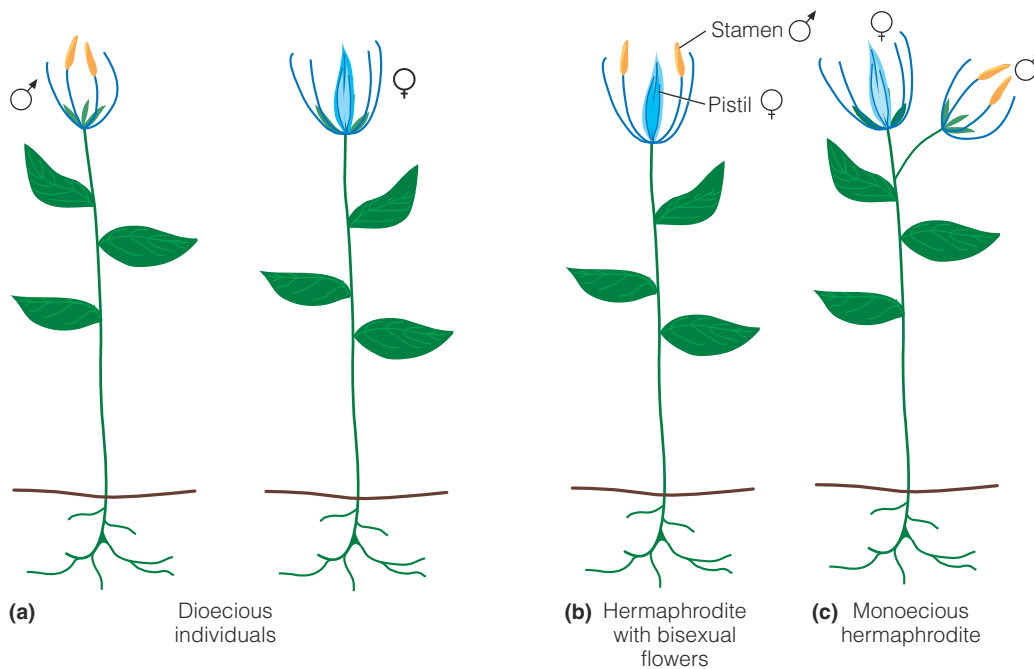


Figure 10.1 Floral structure in (a) dioecious plant (separate male and female individuals), (b) hermaphroditic plant possessing bisexual flowers, and (c) monoecious plant possessing separate male and female flowers.

responds more uniformly to a change in environmental conditions than does a sexually reproducing population. If a change in environmental conditions is detrimental, the effect on the population can be catastrophic.

In contrast, the mixing of genes and chromosomes that occurs in sexual reproduction produces genetic variability to the degree that each individual in the population is genetically unique. This genetic variability produces a broader range of potential responses to the environment, increasing the probability that some individuals will survive environmental changes. But this variability comes at a cost. Each individual can contribute only one-half of its genes to the next generation. It requires specialized reproductive organs that, aside from reproduction, have no direct relationship to an individual's survival. Production of gametes (egg and sperm), courtship activities, and mating are energetically expensive. The expense of reproduction is not shared equally by both sexes. The eggs (ovum) produced by females are much larger and energetically much more expensive than sperm produced by males. As we shall examine in the following sections, this difference in energy investment in reproduction between males and females has important implications in the evolution of life history characteristics.

10.3 Sexual Reproduction Takes a Variety of Forms

Sexual reproduction takes a variety of forms. The most familiar involves separate male and female individuals. It is common to most animals. Plants with that characteristic are called **dioecious** (Greek *di*, “two,” and *oikos*, “home”; **Figure 10.1a**).

In some species, individual organisms possess both male and female organs. They are **hermaphrodites** (Greek *hermaphroditos*). In plants, individuals can be hermaphroditic by

possessing bisexual flowers with both male organs, stamens, and female organs, ovaries (**Figure 10.1b**). Such flowers are termed *perfect*. Asynchronous timing of the maturation of pollen and ovules reduces the chances of self-fertilization. Other plants are **monoecious** (Greek *mono*, “one,” and *oikos*, “home”). They possess separate male and female flowers on the same plant (**Figure 10.1c**). Such flowers are called *imperfect*. This strategy of sexual reproduction can be an advantage in the process of colonization. A single self-fertilized hermaphroditic plant can colonize a new habitat and reproduce, establishing a new population; this is what self-fertilizing annual weeds do that colonize disturbed sites.

Among animals, hermaphroditic individuals possess the sexual organs of both males and females (both testes and ovaries), a condition common in invertebrates such as earthworms (**Figure 10.2**). In these species, referred to as **simultaneous hermaphrodites**, the male organ of one individual is mated with the female organ of the other and vice versa. The result is that a population of hermaphroditic individuals is in theory able to produce twice as many offspring as a population of unisexual individuals.

Other species are **sequential hermaphrodites**. Animals—such as some mollusks and echinoderms—and some plants

Figure 10.2 Hermaphroditic earthworms mating.





Figure 10.3 Parrotfishes (Scaridae) that inhabit coral reefs exhibit sex change. When a large dominant male mating with a harem of females is removed (by a predator or experimenter), within days, the largest female in the harem becomes a dominant male and takes over the missing male's function.

may be males during one part of their life cycle and females in another part. Some fish may be females first, then males. Sex change usually takes place as individuals mature or grow larger. A change in the sex ratio of the population stimulates sex change among some animals. Removing individuals of the other sex initiates sex reversal among some species of marine fish (**Figure 10.3**). Removal of females from a social group among some coral reef fish stimulates males to change sex and become females. In other species, removal of males stimulates a one-to-one replacement of males by sex-reversing females. Among the mollusks, the Gastropoda (snails and slugs) and Bivalvia (clams and mussels) have sex-changing species. Almost all of these species change from male to female.

Plants also can undergo sex change. One such plant is jack-in-the-pulpit (*Arisaema triphyllum*), a clonal herbaceous plant found in the woodlands of eastern North America (**Figure 10.4**). Jack-in-the-pulpit may produce male flowers one year, an asexual vegetative shoot the next, and female flowers the next. Over

Figure 10.4 The jack-in-the-pulpit becomes asexual, male, or female depending on energy reserves. The plant gets its name from the flower stem, or spadix, enclosed in a hoodlike sheath. This fruiting plant is in the female stage.



its life span, a jack-in-the-pulpit may produce both sexes as well as an asexual vegetative shoot but in no particular sequence. Usually an asexual stage follows a sex change. Sex change in jack-in-the-pulpit appears to be triggered by the large energy cost of producing female flowers. Jack-in-the-pulpit plants generally lack sufficient resources to produce female flowers in successive years; male flowers and pollen are much cheaper to produce than female flowers and subsequent fruits.

10.4 Reproduction Involves Both Benefits and Costs to Individual Fitness

To understand how trade-offs function to influence natural selection requires an understanding of the balance between benefits and costs associated with a phenotypic trait. If the objective of reproduction is to maximize the relative fitness of the individual, then the benefit of increasing the number of offspring produced would seem obvious. Yet a central tenet of life history theory is that the behavioral, physiological, and energetic activities involved in reproduction extract some sort of cost to future reproductive success in the form of reduced survival, fecundity, or growth.

There are many examples of various activities involved in reproduction that increase an individual's probability of mortality in addition to the direct physiological costs of reproduction. Activities associated with the acquisition of a mate (see Sections 10.11 and 10.12), defense of a breeding territory (see Chapter 11, Section 11.10), and the feeding and protection of young can reduce the probability of future survival.

The work of Tim Cutton-Block of Cambridge University provides an example of the costs of reproduction in terms of increased probability of future survival. In the development of life tables for a population of red deer in central Scotland, he examined differences in the age-specific patterns of mortality for females—referred to as milk hinds—who have reared a calf to weaning age and those who have not—referred to as yeld hinds (**Figure 10.5**). The higher reproductive costs to milk hinds associated with the care and feeding (lactation) of calves result in higher mortality rates than those observed for yeld hinds (**Figure 10.5a**).

Reproduction can also directly reduce an individual's ability to produce future offspring. The current reproductive expenditure might leave the individual with insufficient energy resources to produce the same number of offspring during future periods of reproduction (**Figure 10.5b**). For example, studies by Sveinn Hanssen of the University of Tromsø in Norway have shown that current reproduction results in reduced future fecundity in eider ducks. The common eider (*Somateria mollissima*) is a long-lived sea duck whose females do not eat during the incubation period. As a result, the reproductive effort of the female results in an increased loss of body mass and reduced immune function.

In a four-year study, Richard Primack and Pamela Hall of Boston University examined the costs of reproduction in

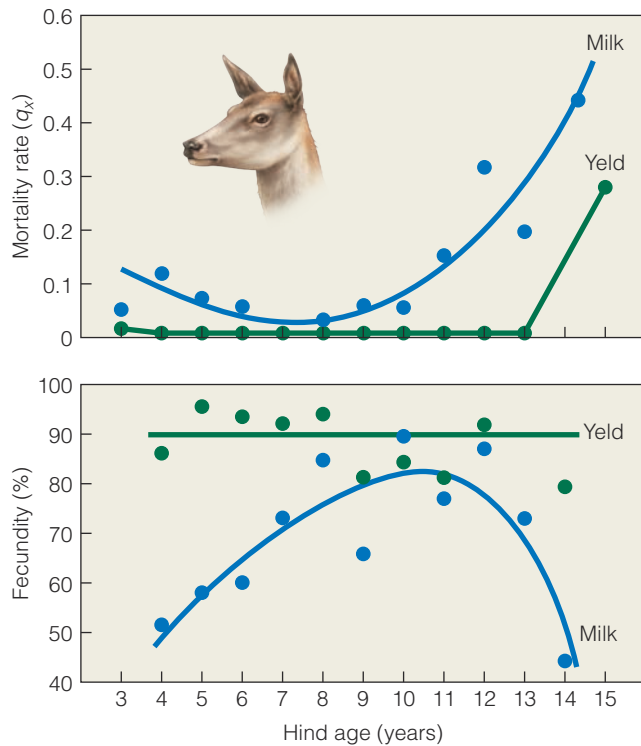


Figure 10.5 Example of the costs of reproduction. (a) Age-specific mortality rates for red deer hinds (milk hinds) that have reared a calf to weaning and those that failed to produce or rear a calf (yield hinds) show the effects of breeding on survival (measured as overwinter mortality). Increase in mortality rate is associated with declining condition (measured in terms of kidney fat) resulting from the energetic costs of lactation. (b) Milk hinds are less likely to conceive the following year than yield hinds. (Clutton-Brock 1984.)

the pink lady's slipper orchid (*Cypripedium acaule*). In two eastern Massachusetts populations, the researchers randomly assigned plants to be hand pollinated (increased reproduction) or left as controls, and the treatments were repeated in four successive years. By the third and fourth years of the study, the high cost of reproduction resulted in a lower growth and flowering rate of hand-pollinated plants in comparison with the control plants. For an average-sized plant, the production of fruit in the current year results in an estimated 10–13 percent decrease in leaf area and a 5–16 percent decrease in the probability of flowering in the following year. Increased allocation of resources to reproduction relative to growth diminished future fecundity (Figure 10.6).

Allocation to reproduction has been shown to reduce allocation to growth in a wide variety of plant and animal species (Figure 10.7). In many species, there is a direct relationship between body size and fecundity (Figure 10.8). As a result, an individual reproducing earlier in age will produce fewer offspring per reproductive period than an individual that postpones reproduction in favor of additional growth.

The act of reproduction at a given age, therefore, has potential implications to both age-specific patterns of mortality

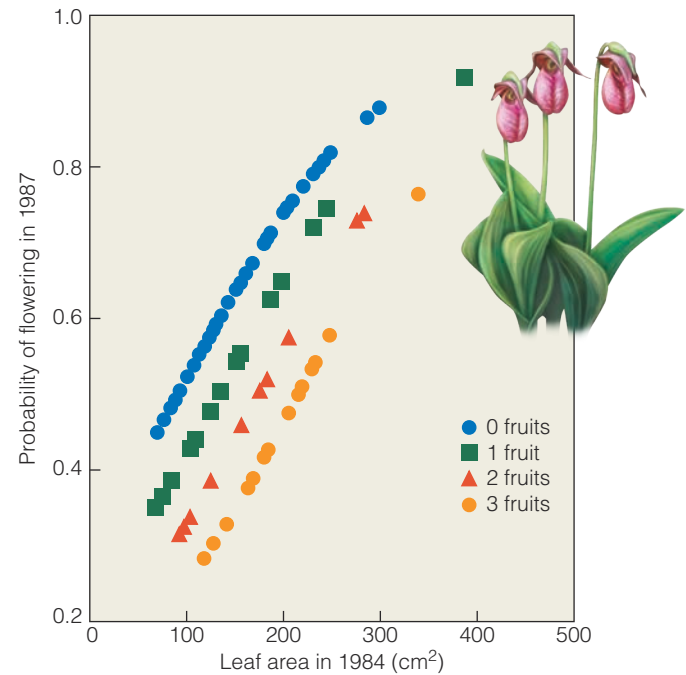


Figure 10.6 Example of cost of reproduction in the pink lady's slipper orchid (*Cypripedium acaule*): the probability of a plant flowering in 1987 based on its initial size (leaf area in cm^2 in 1984) and allocation to reproduction (the number of fruits produced for the period of 1984–1986). The probability of flowering increases with plant size, but for a given size plant, the probability of flowering declines as a function of previous allocation to reproduction (number of fruits produced during the period of 1984–1986). (Adapted from Primack and Hall 1990.)

Interpreting Ecological Data

Q1. What is the approximate difference in the probability of flowering in 1987 for individuals with a leaf area of 200 cm^2 that produced zero fruits and three fruits during the period from 1984 to 1986? What does this tell you about the impact of the costs of past reproduction on future prospects of reproduction?

Q2. According to the preceding figure, the probability of an individual with leaf area of 100 cm^2 that produced zero fruits over the past three years (1984–1986) flowering in the following year (1987) is approximately 0.5 (or 50 percent). How large would an individual that bore three fruits over the past three years have to be to have the same probability of flowering?

(survivorship) and fecundity (birthrate) moving forward. For this reason, the age at which reproduction begins—the age at maturity—is a key aspect of the organism's life history.

10.5 Age at Maturity Is Influenced by Patterns of Age-Specific Mortality

When should an organism begin the process of reproduction? Some species begin reproduction early in their life cycle, whereas others have a period of growth and development before

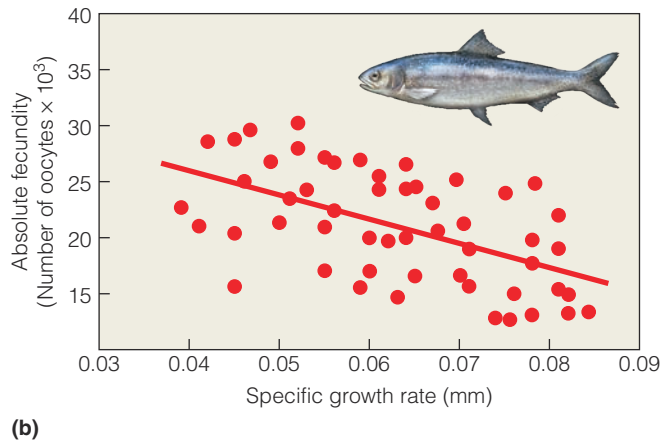
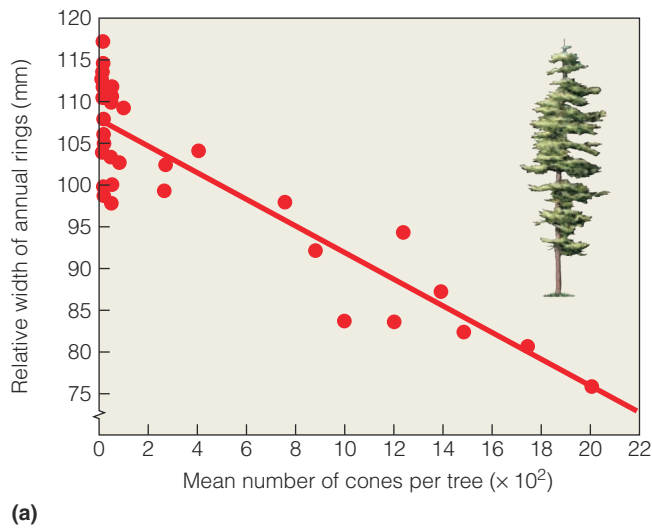


Figure 10.7 (a) Douglas fir trees (*Pseudotsuga menziesii*) exhibit an inverse relationship between the allocation to reproduction (number of cones produced) and annual growth (as measured by radial growth). (b) The relationship between specific growth rate (natural log of the increase in total body length between February and June) and absolute fecundity (measured as the number of oocytes) of three-year-old round sardinella. ([a] Adapted from Eis 1965; [b] Adapted from Tsikliras et al. 2007.)

the onset of reproduction. If natural selection functions to maximize the relative fitness of the individual, then the age and size at maturity are optimized when the difference between the costs and benefits of maturation at different ages and sizes is maximized. That is when the “payoff” in the fitness of the individual is greatest. An important component of this evolution is the age-specific pattern of mortality because it both shapes and is shaped by the age-specific expenditures of reproductive effort.

To explore how natural selection can function to influence the age at maturity, let’s return to think about the age-specific patterns of survival and fecundity that we developed in the previous chapter, that is, the patterns of survival and fecundity that

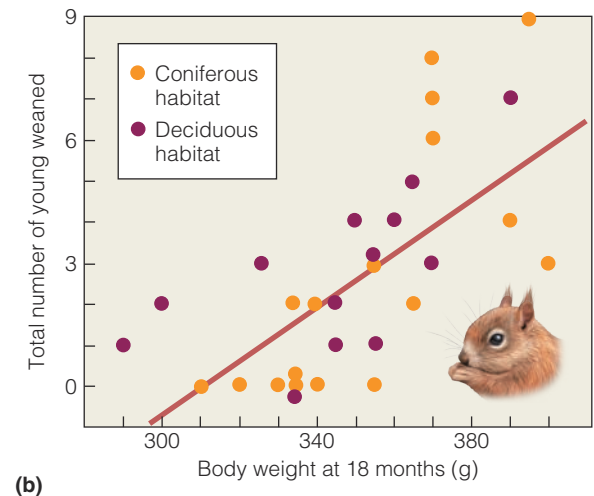
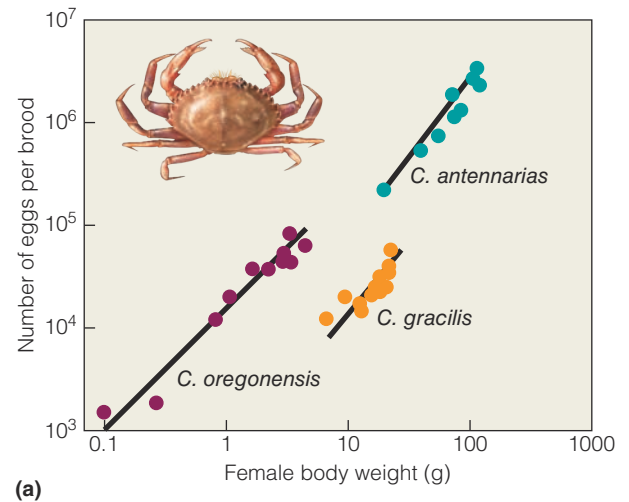


Figure 10.8 (a) Relationship between number of eggs per brood and body weight for three crab species of the genus *Cancer*. (b) Lifetime reproductive success of the European red squirrel is correlated with body weight in the first winter as an adult (age of 18 months).

([a] Data from Hines 1991; [b] Adapted from Wauters and Dhondt 1989.)

determine the trajectory of population growth (Table 10.1; see also Section 9.6). Recall that the first column labeled x shows the age or age class of individuals in the population. The column labeled s_x shows the age-specific survival rates (the probability of an individual of age x surviving to age $x + 1$), and column b_x represents the average number of female offspring produced by an individual female of age x . The three columns have been divided into three distinct age categories relating to reproduction: prereproductive, reproductive, and postreproductive. Prereproductive age categories represent juveniles, whereas the reproductive and postreproductive categories are referred to as adults. The age of maturity then

Table 10.1

x	s _x	b _x	
0	0.05	00.0	} Prereproductive (Juvenile)
1	0.05	00.0	
2	0.10	00.0	
3	0.25	25.0	} Reproductive (Adult)
4	0.45	30.0	
5	0.50	30.0	
6	0.50	25.0	
7	0.45	20.0	
8	0.40	15.0	} Postreproductive (Adult)
9	0.20	00.0	
10	0.00	00.0	

represents the transition from juvenile to adult, or the age at which first reproduction occurs. In our example, we assume that the organism reproduces repeatedly following the onset of maturity until postreproductive age is achieved; however, this is not always the case, as we will discuss later. Our objective is to understand that both extrinsic and intrinsic factors influence the evolution of age at maturity.

Natural selection will favor those individuals whose age at maturity results in the greatest number of offspring produced over the lifetime of an individual. Consider a simple hypothetical example of a species that continues to grow with age only until it reaches sexual maturity and then begins to reproduce. As with the examples presented in Figure 10.8, assume that fecundity increases with body weight—the larger the individual female, the greater the number of offspring produced per time period (reproductive event). Now assume that individuals within the population vary in the age at which they achieve maturity. As a result of differences in body weight, a female that begins to reproduce at age 3 will produce 10 offspring per year over the duration of her lifetime, whereas a female that delays reproduction until age 5 will have a 50 percent greater fecundity, or 15 offspring per year (Figure 10.9). Therefore, we can calculate the cumulative number of offspring produced at any point in each female’s life by summing the number of offspring from the onset of maturity to that age (see Figure 10.9). Note in Figure 10.9 that the female that delayed maturity until year 5 has produced a greater number of offspring over her lifetime. Thus, natural selection should favor delayed maturity. However, this conclusion assumes that the females live to their maximum age (12 years). In fact, before age eight the female that matured early has a greater cumulative number of offspring, and it is only if females survive past year eight that the strategy of delayed maturity increases fitness. Recall the difference between gross and net reproductive rate presented previously (Section 9.6). The value obtained by summing the values in the b_x column as was done in this example is a

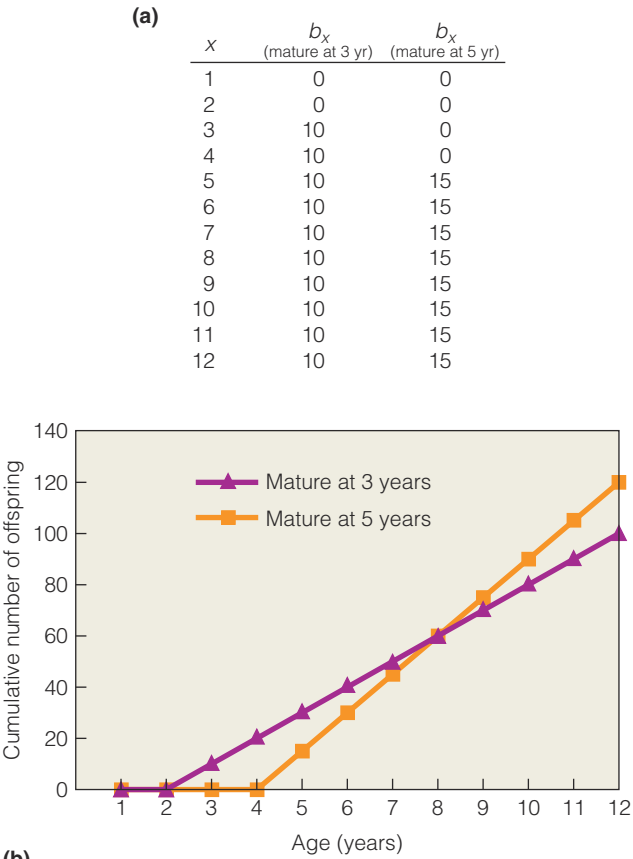


Figure 10.9 Comparison of cumulative reproduction over the lifetime of two individuals that differ in age at maturity. Both individuals continue to grow only until the onset of maturity. (a) One individual matures at age three and has a fixed fecundity rate of 10 offspring per year. The other individual matures at age five, and the additional allocation to growth and increased body size results in a 50 percent increase in fecundity (average of 15 offspring per year). (b) Until age eight, the individual that matures at age three has a greater accumulated fecundity. From age eight forward, however, the individual that matures at age five has the greater accumulated reproduction.

measure of gross reproductive rate, and the strategy of delayed maturity is clearly the winner in terms of fitness. However, the true measure of reproductive rate is net reproductive rate (R_0), as it considers both the age-specific values of fecundity (b_x) and the age-specific values of survivorship (l_x). If survival beyond age eight is an improbable event for this species, then the strategy of early maturity results in the greater fitness.

As the preceding hypothetical example demonstrates, the primary fitness advantage of delaying maturity is the larger initial body size obtained by individuals when they first reproduce. The primary cost of delaying reproduction (late maturity) is the increased risk of death before reproduction, or death before the advantage of increased fecundity as a result of delayed maturity are fully realized—in this example, death before age eight. If one assumes that natural selection acts on