



Chapter Twelve

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n a rare sunny day in temperate rain forest, a redwood tree, *Sequoia sempervirens*, shades a nearby stream. Bathed in fog all summer, soaked by rain during fall, winter, and spring, the redwood has lived through 2,000 annual cycles (see fig. 2.27). The tree was well established when Rome

invaded Britain and had produced seeds for 500 years when William the Conqueror invaded the island from across the English Channel. It was 1,800 years old when rag tag colonials wrenched an American territorial prize from William's heirs, claiming it as their own country. Within a mere century the descendants of the colonial rebels had expanded their territory 2000 miles westward and were chopping down redwood trees for lumber. Other human populations had long lived near the base of the tree and had cut some trees. However, no population had been so relentless as the newcomers who stripped vast areas of all trees. Somehow, before all the redwoods were gone the cutting stopped and the grove of the giant redwood was protected. With luck the tree would live through several more centuries of summer fog and winter rain, during which the human order of the world would surely change many times more.

On this summer morning other life was stirring in the nearby stream. A female mayfly along with thousands of others of her species were shedding their larval exoskeletons as they transformed from their robust crawling aquatic stage to graceful flying adults (fig. 12.1). As a larva the mayfly had lived in the stream for a year, but her adult stage would last just this one day, during which she would mate, deposit her eggs in the stream, and then die. She had just this one chance to successfully complete her life cycle. For an adult mayfly, there is no tomorrow—one chance and no more. As the mayflies swarmed, some would be eaten by birds nesting in alder trees that grew along the stream, and some would be caught by bats that found roosting sites on the giant redwood. Some of the mayflies would be eaten by fish that they had successfully eluded for a year of larval life, and still others would be snared by spiders that spun their webs in azalea shrubs that grew between the alders and the redwood. However, this particular mayfly escaped all predators, mated, and laid her eggs.



FIGURE 12.1 Adult mayflies generally live one day only.

Spent by the effort of depositing her eggs, the mayfly was caught by the current and washed downstream. Fifty meters from where she emerged that morning, the mayfly was taken from the surface by a trout as she floated past an old redwood log where the trout sheltered. The small splash of the feeding trout caught the attention of a man and a woman who had been studying the stream. They knew the stream well and knew the pool where the big trout lived and they knew the trout, which they had tried to catch many times. Their grandparents' generation had cut the redwood forests. Later, their parents had worked to protect this remnant grove. The man and woman had played in the grove as children and courted there as young adults. Now that their own children were grown, they fished the stream frequently, sharing the place once again.

Redwood, mayfly, fish, and humans, lives intertwined in a web of ecological relationships but vastly different in scale and timing. All four are players in an ecological and evolutionary drama stretching into a vast past and into an unknown future. Made of the same elements and with their genetic inheritance encoded by DNA of the same basic structure, the four species have inherited vastly different lives. While the redwood has produced seeds numbering in the millions over a lifetime that has stretched for millennia, the mayfly spends a year in the stream and then emerges to lay eggs that will number in the hundreds. The trout's spawn has numbered in the thousands, deposited during the several years of her life. Meanwhile the man and woman have produced two children during their lifetime, investing time and energy into them over a period of decades.

What are the selective forces that created and maintain this vast range of biology? Under what conditions will organisms mature at an early age and small size instead of later at a larger size? What are the costs and benefits of producing millions of tiny offspring, such as the seeds of the redwood tree, versus a few that are large and well cared for? These are the sorts of questions pondered by ecologists who study **life history**. Life history consists of the adaptations of an organism that influence aspects of its biology such as the number of offspring it produces, its survival, and its size and age at reproductive maturity. Chapter 12 presents case histories bearing on some of the central concepts of life history ecology.

CONCEPTS



- Because all organisms have access to limited energy and other resources, there is a trade-off between the number and size of offspring; those that produce larger offspring are constrained to produce fewer, while those that produce smaller offspring may produce larger numbers.

- Where adult survival is lower, organisms begin reproducing at an earlier age and invest a greater proportion of their energy budget into reproduction; where adult survival is higher, organisms defer reproduction to a later age and allocate a smaller proportion of their resources to reproduction.
- The great diversity of life histories may be classified on the basis of a few population characteristics, such as fecundity or number of offspring, m_x , survival, l_x , and age at reproductive maturity, α .

CASE HISTORIES: offspring number versus size



Because all organisms have access to limited energy and other resources, there is a trade-off between the number and size of offspring; those that produce larger offspring are constrained to produce fewer, while those that produce smaller offspring may produce larger numbers.

The discussions of photosynthetic response by plants (see figs. 6.19, 6.20) and functional response by foraging animals (see figs. 6.21, 6.22, 6.23) led us to conclude that all organisms take in energy at a limited rate. As we saw, rate of energy of intake is limited either by conditions in the external environment, such as food availability, or by internal constraints such as the rate at which the organism can process food. These constraints led in turn to the **principle of allocation**. The principle of allocation underscores the fact that if an organism uses energy for one function such as growth, it reduces the amount of energy available for other functions such as reproduction. This tension between competing demands for resources leads inevitably to trade-offs between functions. One of those is the trade-off between number and size of offspring. Organisms that produce many offspring are constrained, because of energy limitation, to produce smaller offspring (seeds, eggs, or live young). Viewed from the opposite perspective, organisms that produce large, well cared for offspring are constrained to produce fewer. Let's begin our review of case histories bearing on this generalization with a survey of patterns among fish, a vertebrate group with especially large variation in life history characteristics.

Egg Size and Number in Fish

Because of their great diversity (more than 20,000 existing species) and the wide variety of environments in which they live, fish offer many opportunities for studies of life history. Kirk Winemiller (1995) pointed out that fish show more

variation in many life history traits than any other group of animals. For instance, the number of offspring they produce per brood, that is their **clutch size**, ranges from the one or two large live young produced by mako sharks to the 600,000,000 eggs per clutch laid by the ocean sunfish. However, many variables other than offspring number and size change from sharks to sunfish. Therefore, more robust patterns of variation can be obtained by analyzing relationships within closely related species, such as within families or genera.

In a study of gene flow among populations of darters, small freshwater fish in the perch family, or Percidae, Tom Turner and Joel Trexler tried to determine the extent to which life history differences among species might influence gene flow between populations. Turner and Trexler (1998) pointed out that in such a study, it is best to focus on a group of relatively closely related organisms with a shared evolutionary history. They were particularly interested in determining the relationship between egg size and egg number, or **fecundity**, and the extent of gene flow among populations. Fecundity is simply the number of eggs or seeds produced by an organism. Turner and Trexler proposed that gene flow would be higher among populations producing more numerous smaller eggs, that is, among populations with higher fecundity.

Turner and Trexler chose the darters for their studies because they are an ideal study group. Darters are small, streamlined benthic fishes that live in rivers and streams throughout eastern and central North America. Male darters are usually strikingly colored during the breeding season (fig. 12.2). The darters consist of 174 species in three genera within the family Percidae, which makes them one of the most species-rich groups of vertebrates in North America. The most diverse genus, *Etheostoma*, alone includes approximately 135 species. However, despite the fact that the darters as a whole live in similar habitats and have similar anatomy, they vary widely in their life histories. The genera most similar to the ancestors of the darters, *Crystallaria* (one species) and *Percina* (38 species), are larger and produce more eggs than species in the genus *Etheostoma*. However, *Etheostoma* species also vary substantially in their life histories.



FIGURE 12.2 Darters such as this male orangethroat darter form a diverse and distinctive subfamily of fishes within the perch family. They are live only in North America.

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Turner and Trexler sampled 64 locations on streams and rivers in the Ohio, Ozark, and Ouachita Highlands regions of Ohio, Arkansas, and Missouri, the heart of freshwater fish diversity in North America, which supports one of the most diverse temperate freshwater fish faunas on earth. Of the darters they collected at these locations, they chose 15 species, 5 in the genus *Percina* and 10 *Etheostoma* species, for detailed study. Turner and Trexler chose darter species that included a wide range of variation in life history traits, especially variation in body size, number of eggs laid, and egg size.

The species in the study ranged in length from 44 to 127 mm and the number of mature eggs that they produced ranged from 49 to 397. Meanwhile, the size of eggs produced by the study species varied from 0.9 to 2.3 mm in diameter. As they expected, Turner and Trexler found that larger darter species produce larger numbers of eggs (fig. 12.3). Their results also support the generalization that there is a trade-off between offspring size and number. On average, darters that produce larger eggs produce fewer eggs (fig. 12.4).

Turner and Trexler characterized the genetic structure of darter populations using electrophoresis of allozymes produced by 21 different loci (see chapter 8). They chose 21 loci out of 40 that they examined because they were polymorphic. A **polymorphic locus** is one that occurs as more than one allele. In this case each allele synthesizes a different allozyme. Turner and Trexler assessed genetic structure using allelic frequencies. Allelic frequencies were measured as the frequencies of allozymes across the 21 different study loci. Populations with similar allelic frequencies were taken as genetically similar, while those that differed in allelic frequencies were concluded to be different genetically. Gene flow was estimated by the degree of similarity in allelic frequencies between populations.

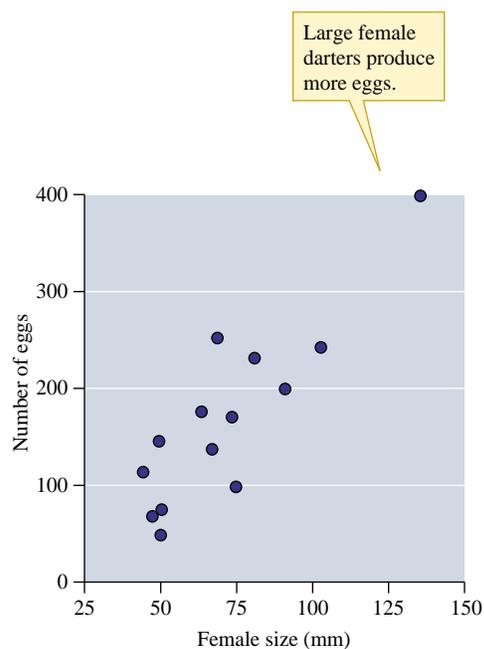


FIGURE 12.3 Relationship between female darter size and number of eggs (data from Turner and Trexler 1998).

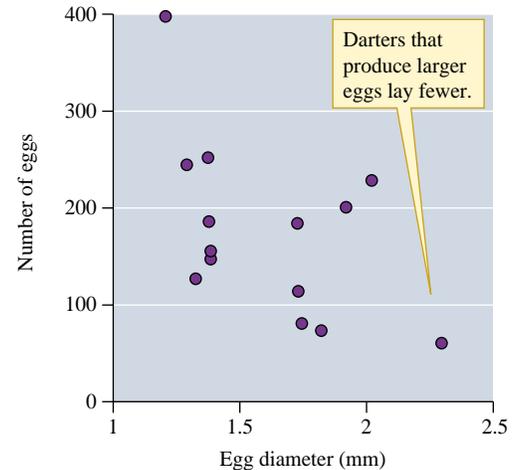


FIGURE 12.4 Relationship between the size of eggs laid by darters and the number of eggs laid (data from Turner and Trexler 1998).

How can the number and kinds of allozymes synthesized by a series of populations be used to determine the extent of gene flow among populations? Turner and Trexler assumed that the populations differing in allelic frequencies have lower gene flow between them than populations that have similar allelic frequencies. In other words, they assumed that genetic similarity between populations is maintained by gene flow, while genetic differences arise in the absence or restriction of gene flow.

What relationship is there between egg size and number and gene flow between populations? Turner and Trexler found a negative relationship between egg size and gene flow but a strong positive relationship of gene flow with the number of eggs produced by females (fig. 12.5). That is, populations of darter species that produce many small eggs showed less difference in allelic frequencies across the study region than did populations that produce fewer larger eggs.

How do differences in egg size and number translate into differences in gene flow among populations. It turns out that the larvae of darters that hatch from larger eggs are larger when they hatch. These larger larvae begin feeding on prey that live on the streambed at an earlier age, and spend less time drifting with the water current. Consequently, larvae hatching from larger eggs disperse shorter distances and therefore carry their genes shorter distances. As a result, populations of species producing fewer larger eggs will be more isolated genetically from other populations. Because of their greater isolation, such populations will differentiate genetically more rapidly compared to populations of species that produce many smaller larvae that disperse longer distances.

Turner and Trexler's study not only provides a case history consistent with the generalization that there is a trade-off between offspring size and number, it also reveals some of the evolutionary consequences of that trade-off.

Trade-offs between offspring number and size have been found in populations of many kinds of organisms. For instance, ecologists have found parallel relationships among terrestrial plants, involving seed number and size.

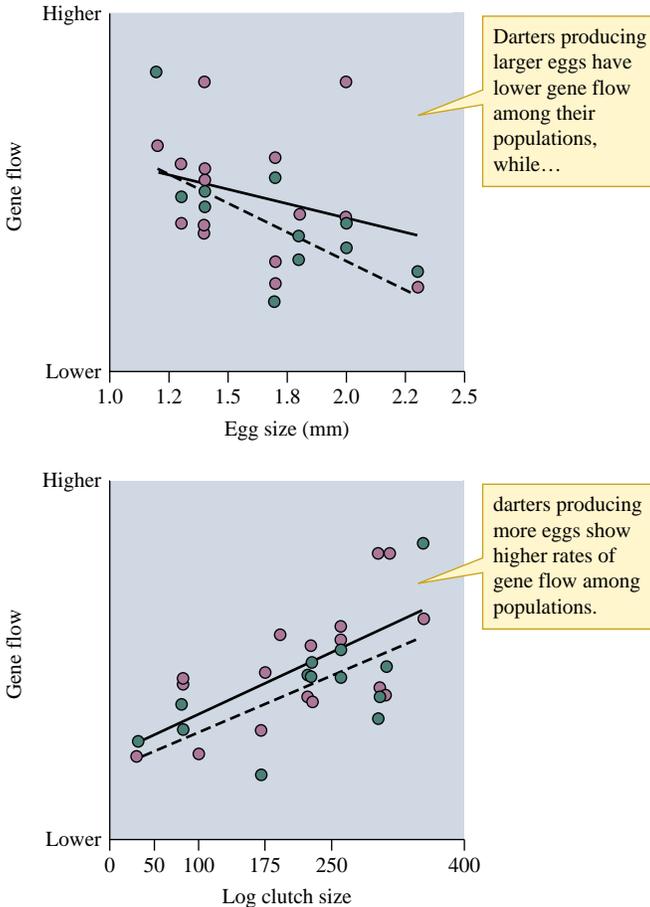


FIGURE 12.5 (Egg size, egg number, and gene flow among darter populations (data from Turner and Trexler 1998).

Seed Size and Number in Plants

Like fish, plants vary widely in the number of offspring they produce, ranging from those that produce many small seeds to those that produce a few large seeds (fig. 12.6). The sizes of seeds produced by plants range over 10 orders of magnitude, from the tiny seeds of orchids that weigh 0.000002 g to the giant double coconut palm with seeds that weigh up to 27,000 g. While some orchids are known to produce billions of seeds, coconut palms produce small numbers of huge seeds. At this scale it is clear that there is a trade-off between seed size and seed number. However, while there are complexities that must be accounted for (Harper, Lovell, and Moore 1970), botanists long ago described a negative relationship between seed size and seed number (Stevens 1932). Figure 12.7 shows the relationship between average seed mass and the number of seeds per plant among species in four families of plants, daisies (Asteraceae), grasses (Poaceae), mustards (Brassicaceae), and beans (Fabaceae). In all four families, species producing larger numbers of seeds on average produced fewer seeds.

Having documented a trade-off between seed size and number, plant ecologists searched for the mechanisms favoring



FIGURE 12.6 A small sample of the great diversity of seed sizes and shapes.

many small seeds in some environments and few larger seeds in others. However, when venturing into the world of plants, the ecologist should be aware of the subtleties of plant biology much of which can be inferred from their morphology. For instance, many characteristics of plants correlate with their **growth form** or life-form, which themselves constitute aspects of the plant life history. Therefore, comparing seed production of orchids and coconut palms, which mixes data from a species having the growth form of an epiphyte (the orchid) and another with the growth form of a tree (the palm), may not be a valid comparison. Such a comparison may not be valid since growth form may itself influence the number and size of seeds produced by plants.

What other aspects of plant biology might influence seed size? As we saw in chapter 10, dispersal is an important facet of the population biology of all organisms, including plants. For instance, figure 10.17 shows the history of maple and hemlock dispersal northward following glacial retreat beginning approximately 14,000 years ago. One of the notable differences shown in figure 10.17 is that maple dispersed northward much faster than hemlock. What is the source of this difference in dispersal rate? Since long-distance dispersal by plants is mainly by means of seeds, we might ask whether there is a relationship between seed characteristics and means of dispersal.

Aware of the potential influence of growth form and dispersal mode on seed characteristics, Mark Westoby, Michelle Leishman, and Janice Lord (1996), studied the relationship between plant growth form and seed size. Their study included the seeds of 196 to 641 species of plants from five different regions. Three of their study regions were in Australia: New South Wales, central Australia, and Sydney; one was in Europe: Sheffield, United Kingdom; and one was in North America: Indiana Dunes. Why did Westoby, Leishman, and Lord include five floras on three continents in their study? By including the plants on three different continents, Westoby, Leishman, and Lord increased their chances of discovering patterns of general importance. If they had worked within a single region, they could not be sure that the patterns they uncovered would hold in other regions.

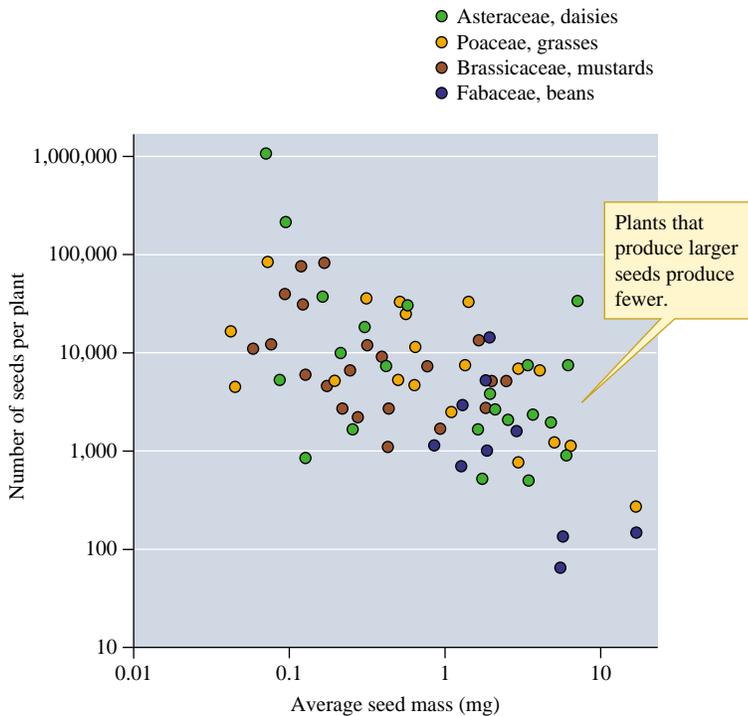


FIGURE 12.7 Relationship between seed mass and seed number (data from Stevens 1932).

Westoby, Leishman, and Lord recognized four plant growth forms. Grasses and grass-like plants, such as sedges and rushes, were classified as **graminoids**. Herbaceous plants other than graminoids were assigned to a **forb** category. Species with woody thickening of their tissues were considered as woody plants. Finally, climbing plants and vines were classified as climbers. The results showed a clear association between seed size and plant growth form (fig. 12.8a). In most of the floras analyzed by Westoby and his colleagues, the smallest seeds were produced by graminoid, plants followed by the seeds produced by forbs. In all five study regions, woody plants produce seeds that are far larger than those produced by either graminoids or forbs. However, the largest seeds in all regions are produced by vines. The researchers found that the seeds produced by woody plants and vines in the five floras were on average approximately 10 times the mass of seeds produced by either graminoid plants or forbs.

Westoby and his coauthors recognized six dispersal strategies. They classified seeds with no specialized structures for dispersal as unassisted dispersers. If seeds had hooks, spines, or barbs, they were classified as **adhesion-adapted**. Meanwhile, seeds with wings, hairs, or other structures that provide air resistance were assigned to a wind-dispersed category. Animal dispersed seeds in the study included ant-dispersed, vertebrate-dispersed, and scatterhoarded. Westoby, Leishman, and Lord classified seeds with an **elaiosome**, a structure on the surface of some seeds generally containing oils attractive to ants, as ant-dispersed. Seeds with an **aril**, a fleshy covering of some seeds that attracts birds and other ver-

tebrates, or with flesh were classified as vertebrate-dispersed. Finally they classified as **scatterhoarded** those seeds known to be gathered by mammals and stored in scattered caches or hoards.

Westoby, Leishman, and Lord also found that plants that disperse their seeds in different ways tend to produce seeds of different sizes (fig. 12.8b). Plants that they had classified as unassisted dispersers produced the smallest seeds, while wind dispersed seeds were slightly larger. Adhesion-adapted seeds were of intermediate size, while animal-dispersed seeds were largest. Ant-dispersed seeds were the next largest, vertebrate-dispersed seeds were somewhat larger, and scatterhoarded were the largest by far. Westoby and his team point out that between 21% and 47% of the variation in seed size in the five floras included in their study is accounted for by a combination of growth form and mode of dispersal.

The analyses by Westoby and his colleagues show that both plant growth form and dispersal mode are associated with differences in seed size among plants. Impressively, the relationships between seed size and both growth form and dispersal mode were consistent across widely separated geographic regions. However, Westoby, Leishman, and Lord pointed out that their analysis uncovered wide variation in seed size among plants in all regions. What are the factors that maintain variation in seed size? To maintain such variation, there must be advantages and disadvantages of producing either large or small seeds. What are those advantages and disadvantages? Plants that produce small seeds can produce greater numbers of seeds. Such plants seem to have an advantage where disturbance rates are high and where plants with the capacity to colonize newly opened space appear to thrive. Though plants that produce large seeds are constrained to produce fewer, large seeds produce seedlings that survive at a higher rate in the face of environmental hazards. Those hazards include competition from established plants, shade, defoliation, nutrient shortage, deep burial in soil or litter, and drought.

Anna Jakobsson and Ove Eriksson (2000) of Stockholm University studied the relationships between seed size, seedling size, and seedling recruitment among herbs and grasses living in seminatural grasslands in southeastern Sweden. To estimate the influence of seed size and seedling size, Jakobsson and Eriksson germinated seeds in pots containing a standardized soil mix. The pots were maintained in a greenhouse under standardized conditions and seedlings were harvested and weighed 3 weeks after **germination**. Germination is the process by which seeds begin to grow or develop, producing the small plant called a seedling in the process. Why did Jakobsson and Eriksson conduct this experiment in a greenhouse? The main reason was that their ability to control environmental conditions such as soil type, moisture availability, and temperature in the greenhouse ensured that differences in seedling size would be due mainly to differences in seed size and not due to differences in the environments in which the seeds germinated. The

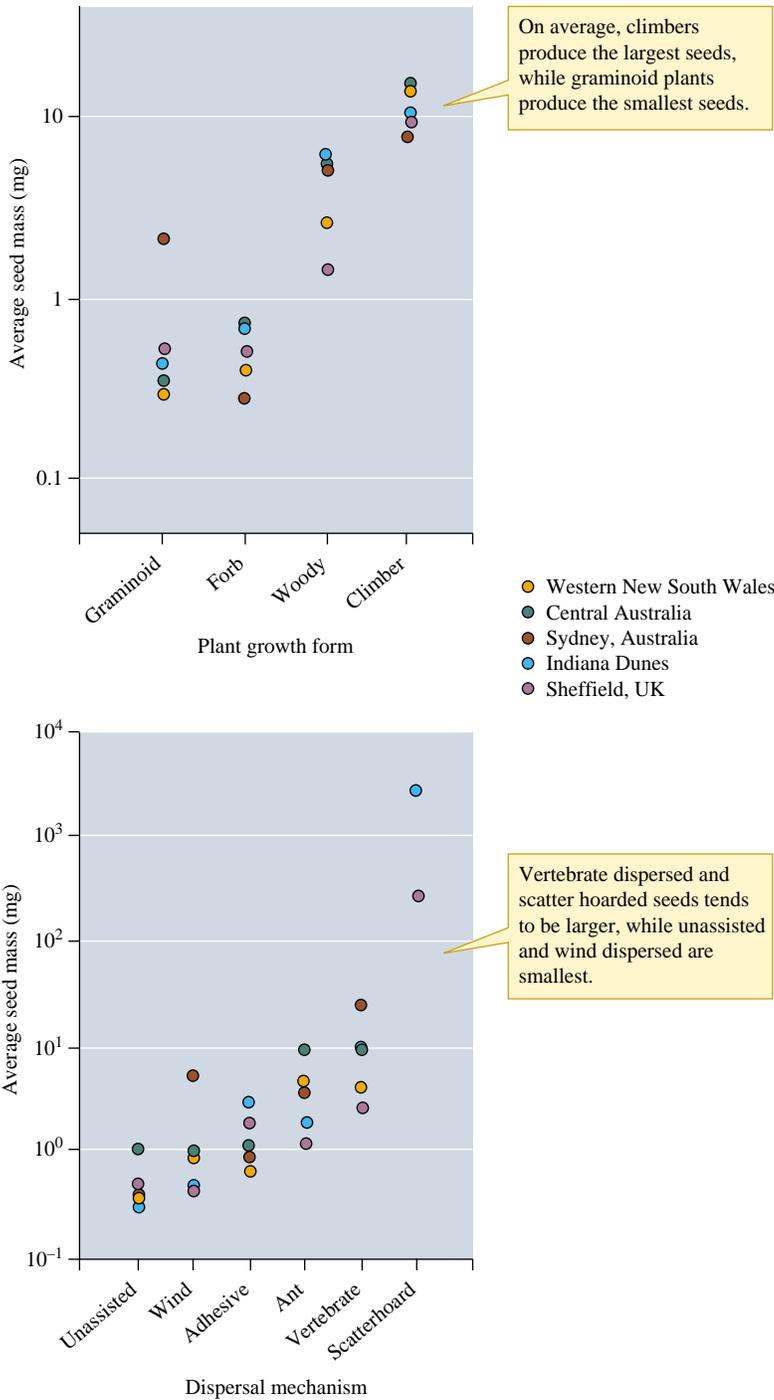


FIGURE 12.8 Plant growth form and dispersal mechanism and seed mass (data from Westoby, Leishman, and Lord 1996).

Q: add "(a)" and "(b)" labels to art?

results of this portion of the study showed clearly that larger seeds produced larger seedlings (fig. 12.9).

Jakobsson and Eriksson also investigated the relationship between seed size and recruitment among 50 plant species living in the meadows of their study region, using a field experiment. At their field sites, Jakobsson and Eriksson planted the seeds of each species in 14 small 10 × 10 cm plots. Each plot was sown with 50–100 seeds of the study species. They left

half of the study plots undisturbed, while the other plots were disturbed before planting by scratching the soil surface and removing any accumulated litter. In addition to the 14 plots where seeds were sown, Jakobsson and Eriksson established control plots where they did not plant seeds. Again, half of these were disturbed and half left undisturbed. Why did Jakobsson and Eriksson need to establish these control plots? The control plots allowed them to estimate how much germination of each species would occur in the absence of their sowing new seeds. The seeds of many species can lie dormant in soils for long periods of time and additional seeds of their study species might have dispersed into the study plots during the experiment. Therefore, without the control plots, Jakobsson and Eriksson would have no way of knowing if the seedlings they observed had grown from the seeds they had sown or from other seeds.

Of the 50 species of seeds planted, the seeds of 48 species germinated and those of 45 species established recruits. Jakobsson and Eriksson observed no recruitment of any of the study species on the control plots. Therefore they could be confident that new plants recruited into their experimental plots came from seeds that they had planted. Though plants recruited to both undisturbed and disturbed plots, the number of recruits was generally higher in disturbed plots. Further, eight species of plants recruited only on disturbed plots.

What role did differences in seed size play in the rate of recruitment by different species? Jakobsson and Eriksson calculated recruitment success in various ways. One of the most basic ways that they calculated recruitment was by dividing the total number of recruits by the total number of seeds of a species that they planted, giving the proportion of seeds sown that produced recruits. While 45 of 50 species established new recruits in the experimental plots, the rate at which they established varied among species from approximately 5% to nearly 90%. Jakobsson and Eriksson found that differences in seed size explained much of the observed differences in recruitment success among species (fig. 12.10). On average, larger seeds, which produce larger seedlings, were associated with a higher rate of recruitment. Therefore it appears that by investing

more energy into a seed, the maternal plant increases the probability that the seed will successfully establish itself as a new plant. This advantage associated with large seed size is probably very important in environments such as the grasslands studied by Jakobsson and Eriksson, where competition with established plants is likely to be high.

Jakobsson and Eriksson focused their work on grasslands where the principal growth forms were, using the

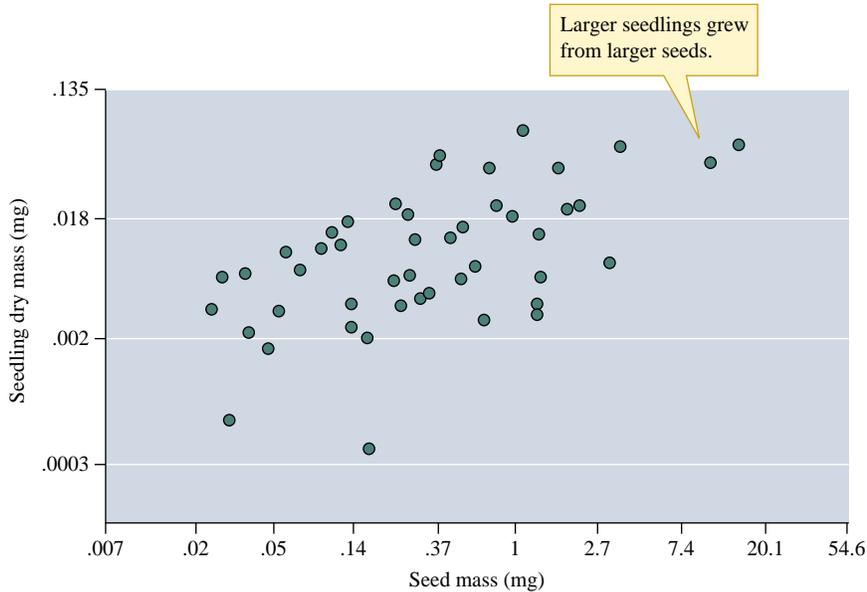


FIGURE 12.9 Seed mass and seedling mass among grassland plants in Sweden (data from Jakobsson and Eriksson 2000).

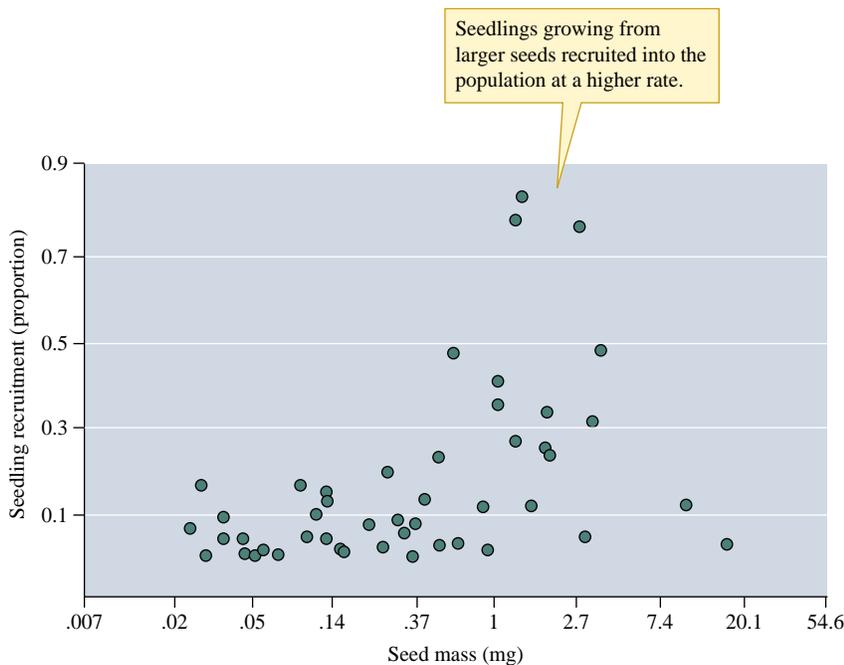


FIGURE 12.10 Seed mass and recruitment rates in grassland plants (data from Jakobsson and Eriksson 2000).

classification presented in figure 12.8a, graminoid or forbs. However, as shown in figure 12.8a, woody plants and vines produce substantially larger seeds than herbaceous graminoids and forbs. How might patterns in seed and seedling size vary among woody plants? Kenji Seiwa and Kihachiro Kikuzawa (1991) studied the relationship between seed size and seedling size among tree species native to Hokkaido, the northernmost large island of Japan.

The results of their work and their interpretation of the results provide clear insights into how seed size may improve the ability of seedlings of surviving environmental hazards. Seiwa and Kikuzawa were especially focused on the influences of shade on seedling establishment.

The trees studied by Seiwa and Kikuzawa were all broad-leaved deciduous trees that grow in the temperate deciduous forests of Hokkaido either on mountain slopes between 100 and 200 m in altitude or in riparian forests. The fruits of all the study species were collected from trees growing in the arboretum of the Hokkaido Forest Experimental Station. In the laboratory the research team removed any fruit pulp from the seeds, washed them, and then allowed them to air dry for 24 hours. Seiwa and Kikuzawa then estimated average seed mass by weighing one to five groups of 100 to 1000 randomly chosen seeds. A week after they collected the fruits, Seiwa and Kikuzawa planted the seeds they contained in the arboretum nursery at the Hokkaido Forest Experimental Station. They planted seeds at depths of 1 to 2 cm in a clay loam soil and watered three times a week until the soil was saturated.

Seiwa and Kikuzawa's results showed clearly that larger seeds produced taller seedlings (fig. 12.11). They explained this pattern as the result of the larger seeds providing greater energy reserves to boost initial seedling growth. Seiwa and Kikuzawa observed that seedlings from large-seeded species unfolded all of their leaves rapidly in the spring and shed all of their leaves synchronously in the autumn. They concluded that this timing allows the seedlings from large-seeded species to emerge early in the spring before the trees forming the canopy of the forest have expanded their leaves and have shaded the forest floor. Seiwa and Kikuzawa also pointed out that rapid growth would help seedlings penetrate the thick litter layer on

the floor of deciduous forests and help them establish themselves as part of the forest understory.

In addition to showing variation in the number and sizes of offspring produced, organisms also show a great deal of variation in the age at which they begin reproducing. They also differ greatly in the relative amount of energy they allocate to reproduction versus growth and maintenance. Over the years life history ecologists have observed patterns in age of

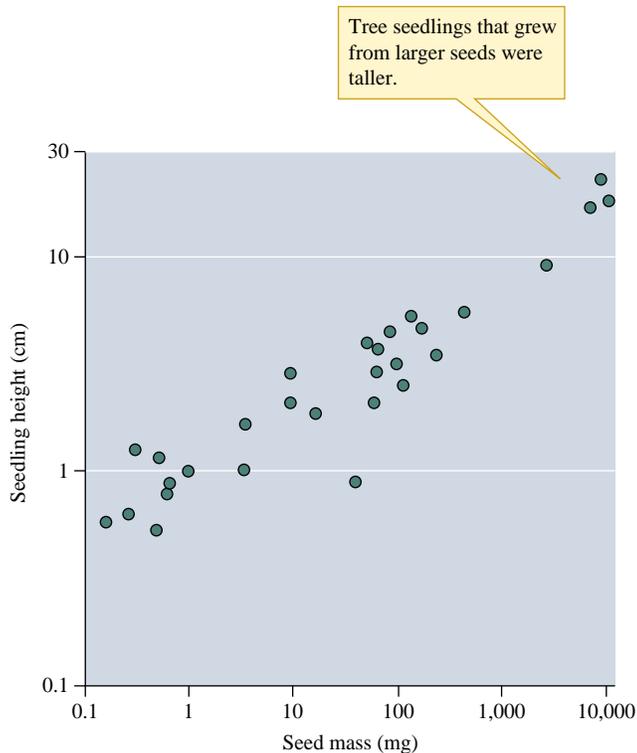


FIGURE 12.11 Relationship between seed mass and seedling height among trees (Seiwa and Kikuzawa 1991).

reproductive maturity and relative investment in reproduction among species that support some broad generalizations.

CASE HISTORIES: adult survival and reproduction allocation



Where adult survival is lower, organisms begin reproducing at an earlier age and invest a greater proportion of their energy budget into reproduction; where adult survival is higher, organisms defer reproduction to a later age and allocate a smaller proportion of their resources to reproduction.

Is there a relationship between the probability of an organism living from one year to the next and the age at which the organism begins reproducing? What environmental factors are responsible for variation in age at maturity and the amount of energy allocated to reproduction, which has been called **reproductive effort**? (Reproductive effort is the allocation of energy, time, and other resources to the production and care of offspring.) These are two questions central to life history ecology.

Reproductive effort generally involves trade-offs with other needs of the organism, including allocation to growth and maintenance. Because of these trade-offs, allocation to reproduction may reduce the probability that an organism will survive. However, delaying reproduction also involves risk. In this case, an individual that delays reproduction runs the risk of dying before it can reproduce. Consequently, evolutionary ecologists have predicted that variation in mortality rates among adults will be in association with variation in the age of first reproduction, or age of reproductive maturity. Specifically, they have predicted that where adult mortality is higher, natural selection will favor early reproductive maturity; and where adult mortality is low, natural selection has been expected to favor delaying reproductive maturity.

Life History Variation Among Species

The relationship between mortality, growth, and age at first reproduction or reproductive maturity has been examined in a large number of organisms. Early work, which concentrated on fish, shrimp, and sea urchins, suggested linkages between mortality or survival, growth, and reproduction. Richard Shine and Eric Charnov (1992) explored life history variation among snakes and lizards to determine whether generalizations developed through studies of fish and marine invertebrates could be extended to another group of animals living in very different environments.

Shine and Charnov began their presentation with a reminder that, in contrast to most terrestrial arthropods, birds, and mammals, including humans, many animals continue growing after they reach sexual maturity. In addition, most vertebrate species begin reproducing before they reach their maximum body size. Shine and Charnov pointed out that the energy budgets of these other vertebrate species, such as fish and reptiles, are different before and after sexual maturity. Before these organisms reach sexual maturity, energy acquired by an individual is allocated to one of two competing demands: maintenance and growth. However, after reaching sexual maturity, limited energy supplies are allocated to three functions: maintenance, growth, and reproduction. Because they have fewer demands on their limited energy supplies, individuals delaying reproduction until they are older will grow faster and reach a larger size. Because of the increase in reproductive rate associated with larger body size (see fig. 12.3), deferring reproduction would lead to a higher reproductive rate. However again, where mortality rates are high, deferring reproduction increases the probability that an individual will die before reproducing. These relationships suggest that mortality rates will play a pivotal role in determining the age at first reproduction.

Shine and Charnov gathered information from published summaries on annual adult survival and age at which females mature for 16 species of snakes and 20 species of lizards. The

annual rate of adult survival among snakes in their data set ranged from approximately 35% to 85% of the population, while age at reproductive maturity ranged from 2 to 7 years. Meanwhile, the annual rate of lizard survival ranged from approximately 8% to 67% of the population and their age at first reproduction ranged from a little less than 8 months to 6.5 years. Because most of the species they examined were North American and were members of either one family of snakes or one family of lizards, Shine and Charnov urged that their results not be generalized to snakes and lizards generally until other groups from other regions had been analyzed. Regardless of these cautions, the results of Shine and Charnov's study

showed clearly that as survival of adult lizards and snakes increases, their age at maturity also increases (fig. 12.12a).

More recent analyses of the relationship between adult mortality rate and age at maturity among fish species provide additional support for the prediction that high adult survival leads to delayed maturity. Donald Gunderson (1997) explored patterns in adult survival and reproductive effort among 28 populations of fish. Gunderson suggested that there should be a strong relationship between adult mortality in populations and reproductive effort because some combinations of mortality and reproductive effort have a higher probability of persisting than others. For instance, a population showing a

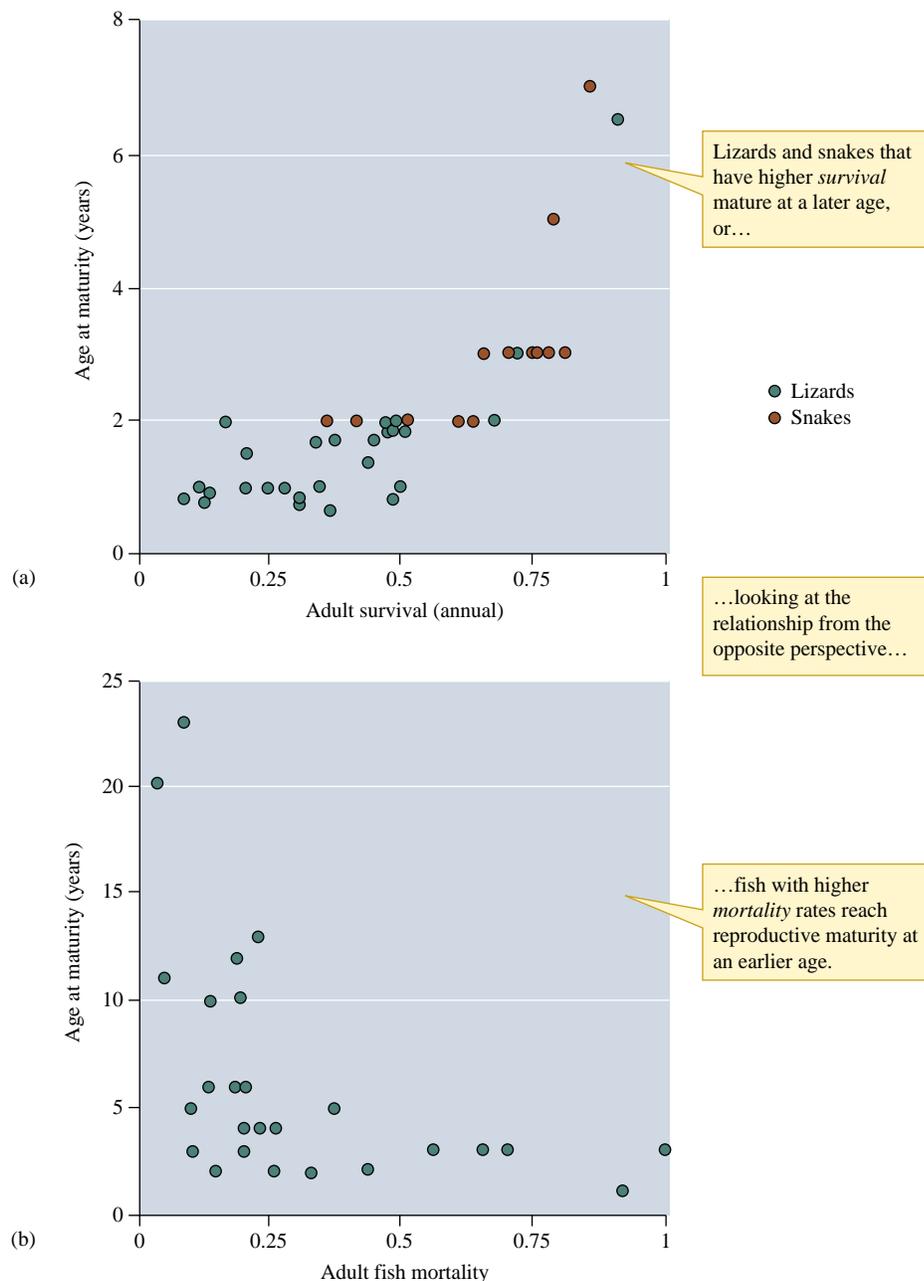


FIGURE 12.12 Relationship between adult survival among lizards and snakes and adult fish mortality and age of reproductive maturity (data from Shine and Charnov 1992 and Gunderson 1997)

combination of high mortality and high reproductive effort would have a higher chance of persisting than one experiencing high mortality but allocating low reproductive effort. The population with this second combination would likely go extinct in a short period of time.

The life history information Gunderson summarized in his analysis included mortality rate, estimated maximum length, age at reproductive maturity, and reproductive effort. Gunderson estimated reproductive effort as each population's **gonadosomatic index**, or **GSI**. GSI was taken as the ovary weight of each species divided by the species body weight and adjusted for the number of batches of offspring produced by each species per year. For example, because the northern anchovy spawns three times per year, the weight of its ovary was multiplied by 3 for calculating its GSI. Meanwhile, the ovary weight for dogfish sharks, which reproduce only every other year, was divided by 2. However, since most of the species included in the analysis spawn once per year, their ovary weights required no adjustment for GSI calculations.

The fish included in Gunderson's analysis ranged in size from the Puget Sound rockfish, which reaches a maximum size of approximately 15 cm, to northeast Arctic cod that reaches a length of 130 cm. The age at maturation among these fish species ranges from 1 year in northern anchovy populations to 23 years in dogfish shark populations. Like Shine and Charnov, Gunderson gathered information about the life histories of the fish in his analysis from previously published papers and several experts on particular fish species. In his table summarizing life history information for the 28 species included in his analysis, Gunderson lists 72 references. In contrast to Shine and Charnov, Gunderson provides estimates of mortality rates rather than survival rates. In addition his estimates are of "instantaneous" mortality rates instead of annual rates. However, like Shine and Charnov, his results show a clear relationship between adult mortality and age of reproductive maturity (fig. 12.12*b*). These results support the idea that natural selection has acted to adjust age at reproductive maturity to rates of mortality experienced by populations.

Gunderson's analysis also gives information on variation in reproductive effort among species. His calculations of a gonadosomatic index, or GSI, for each of the 28 species included in the analysis spanned more than a 30-fold difference from a value of 0.02 for the roughey rockfish to 0.65 for the northern anchovy. What do these numbers mean? Remember that the formula for GSI is ovary weight (multiplied by 3 in the case of the northern anchovy because it spawns three times per year) divided by body weight. In other words, reproductive effort is expressed as a proportion of body weight. Converting these proportions to percentages, we can say that the yearly allocation to reproduction by the roughey rockfish is approximately 2% of its body weight, while the northern anchovy allocates approximately 65% annually! When Gunderson plotted GSI against mortality rates (fig. 12.13), the results supported the prediction from life history theory that species with higher mortality would show higher relative reproductive effort.

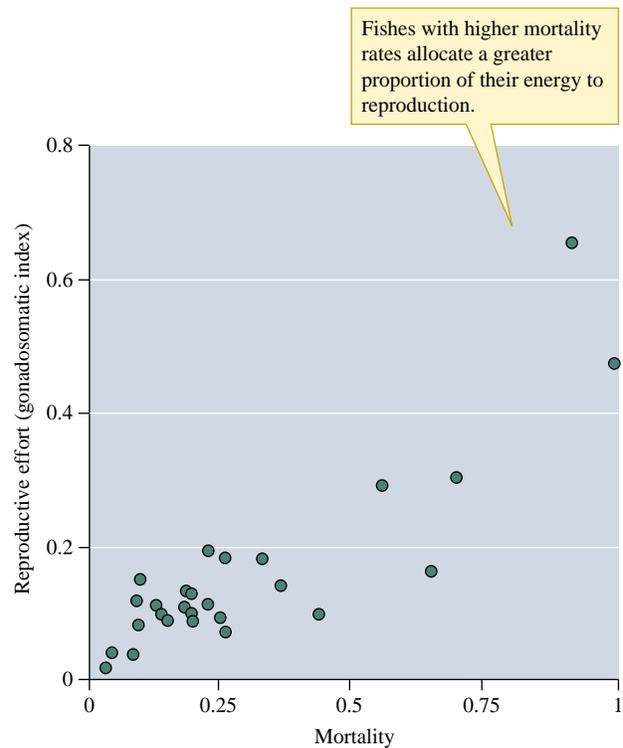


FIGURE 12.13 Relationship between adult fish mortality and reproductive effort as measured by the gonadosomatic index or GSI (data from Gunderson 1997).

Life History Variation Within Species

To this point in our discussion we have emphasized life history differences between species, such as the lizard and snake species compared by Shine and Charnov (fig. 12.12*a*) or the fish species compared by Gunderson (fig. 12.12*b*). Is there evidence that life history differences will evolve within species, where different populations experience different rates of adult mortality? The data set analyzed by Shine and Charnov included 9 populations of the eastern fence lizard, *Sceloporus undulatus*. Variation among those populations indicates that age at maturity within lizard populations increases with increased adult survival. Additional evidence for the evolution of such intraspecific differences comes from a comparative study of several populations of the pumpkinseed sunfish, *Lepomis gibbosus* (fig. 12.14).

Kirk Bertschy and Michael Fox (1999) studied the influence of adult survival on pumpkinseed sunfish life histories. One of the major objectives of their study was to test the prediction by life history theory that increased adult survival, relative to juvenile mortality, favors delayed maturity and reduced reproductive effort. What distinguishes this study from those of Shine and Charnov and Gunderson (fig. 12.12)? Again, Bertschy and Fox focused their attention on variation in life histories among populations of *one species*. In other words, their study goal was to explain the evolution of life history variation within a species.



FIGURE 12.14 A pumpkinseed sunfish, *Lepomis gibbosus*.

Bertschy and Fox selected five populations of pumpkinseed sunfish living in 5 lakes from a group of 27 lakes in southern Ontario, Canada. Fox had previously studied the pumpkinseed sunfish living in these lakes and so they had a considerable basis for choosing study populations. Bertschy and Fox chose lakes that were similar in area and depth and small enough that they had a reasonable chance of estimating mortality rates and variation in other life history characteristics. Their study lakes varied in area from 7.2 to 39.6 ha and in depth from 2.6 to 11 m. Bertschy and Fox also chose lakes that had no major inflows or outflows. Why did they restrict the study to lakes without major inflows or outflows? One reason is that they wanted to avoid as much movement of individuals in and out of their populations as possible. Such movement could obscure the results of natural selection within the lakes for particular life history characteristics.

Bertschy and Fox estimated life history characteristics by sampling approximately 100 pumpkinseed sunfish from each of the 5 study lakes. They caught the fish in their shallow (0.5–2 m depth) littoral habitat using funnel traps and beach seine nets. Bertschy and Fox took their annual population sample in late May or early June just before the beginning or right at the beginning of the spawning season. The individuals caught were sacrificed by placing them in an ice slurry and then freezing them for later analysis. They made several measurements on each individual in their samples, including their age (by counting annual rings in scales), weight (to the nearest 0.1 g), length (in mm), sex, and reproductive status. Because female reproductive effort is largely restricted to egg production while male reproductive effort includes activities such as territory guarding and nest building, Bertschy and Fox studied reproductive traits in females only. A female was considered mature if her ovaries contained

eggs with yolk. The ovaries of mature females were dissected out and weighed to the nearest 0.01 g. Bertschy and Fox represented female reproductive effort using the gonadosomatic index, GSI, which they calculated as $100 \times (\text{ovary mass}) \div (\text{body mass})$, which yields GSI values expressed as percentages rather than as proportions.

Bertschy and Fox used mark and recapture surveys (see Applications and Tools, chapter 9) to estimate the number of adult pumpkinseed sunfish and the age structure (e.g., see figure 10.9) of pumpkinseed populations in each of the study lakes. Ages of fish were estimated from their length using the relationship between length and age of individuals of known age from each population. These surveys, which were conducted each year from 1992 to 1994, gave a basis for estimating rates of adult survival for each age class in each lake's population. The lowest rate, or probability, of adult survival was 0.19, while the highest was 0.65. In other words, the proportion of adults surviving from one year to the next ranged from approximately 1 adult out of 5 (0.19) to about 2 adults out of 3 (0.65). This variation among lakes produced striking differences in the form of survivorship curves (fig. 12.15).

Juvenile survival was estimated by counting the number of pumpkinseed nests and then collecting all the larval fish in a sample of nests. The number of nests in the study lakes varied from 60 to over 1,000 and the number of larval fish produced ranged from approximately 100,000 to over a million. Using their estimate of the number of larvae produced and the number of 3-year-old fish in the same lake, Bertschy and Fox estimated juvenile survival. Juvenile survival to adulthood in the study lakes ranged from 0.004, or about 4 out of 1,000 larvae, to 0.016, or about 16 out of 1,000 larvae. Because they were interested in the relative rates of adult and juvenile survival,

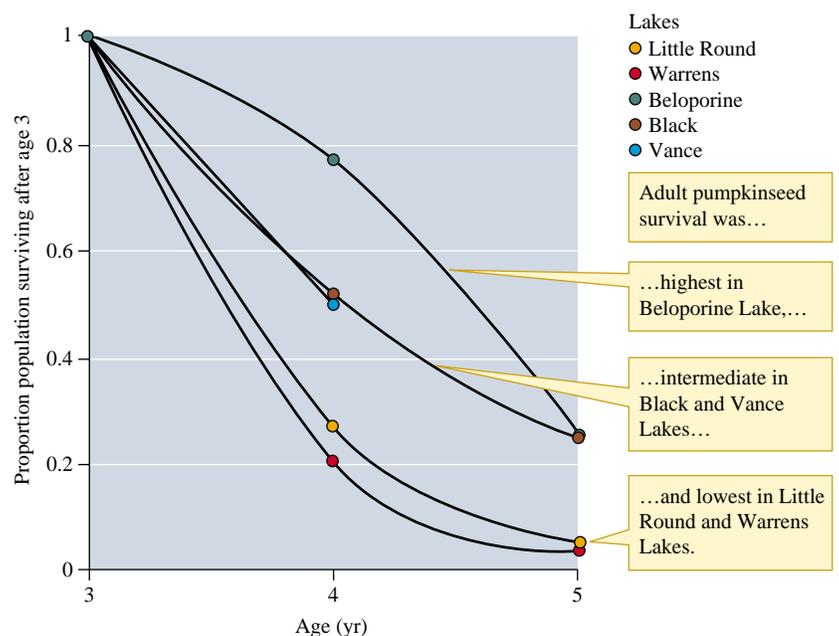


FIGURE 12.15 Pumpkinseed sunfish survival after age three years in five small lakes (data from Bertschy and Fox 1999).

Bertschy and Fox represented survival in their study lakes as the ratio of adult to juvenile survival probabilities. Figure 12.16 shows that this ratio ranged widely among study lakes from a low of 10.6 to 116.8, a tenfold difference among lakes.

Bertschy and Fox found significant variation in most life history characteristics across their study lakes. Pumpkinseed sunfish matured at ages ranging from 2.4 to 3.4 years in the different study lakes and they showed reproductive investments (gonadosomatic indexes or GSI) ranging from 6.9% to 9.3%. The relationship between survival rate and age at maturity found by Bertschy and Fox suggests that populations with higher adult survival mature at a greater age (fig. 12.17). The correlation between survival rate and age at maturity was not close enough to be statistically significant; however, the relationship between adult survival and reproductive effort was very clear and highly significant (fig. 12.18). The patterns of life history variation across the pumpkinseed populations studied by Bertschy and Fox support the theory that where adult survival is lower relative to juvenile survival, natural selection will favor allocating greater resources to reproduction.

As we explored the relationship between offspring size and number and the influence of mortality on the timing of maturation and reproductive effort, we've accumulated a large body of information on life histories. Let's step back now and try to organize that information to make it easier to think about life history variation in nature. Several researchers have proposed classification systems for life histories.

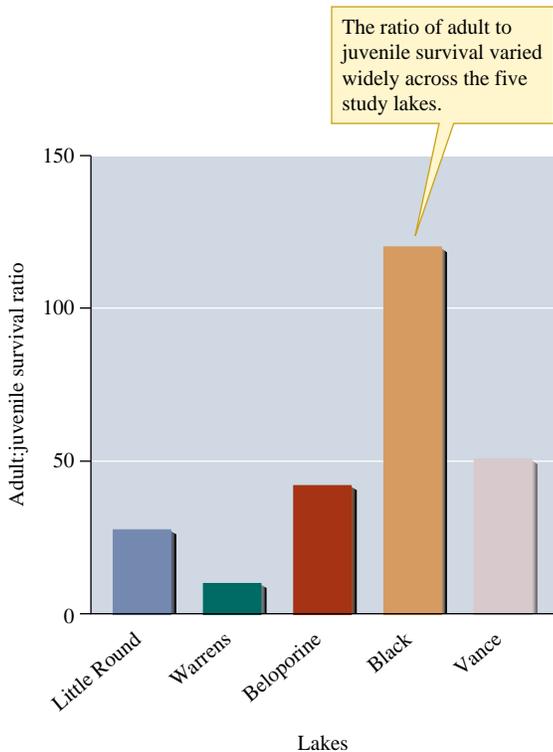


FIGURE 12.16 Ratio of adult to juvenile survival in pumpkinseed sunfish populations in five small lakes (data from Bertschy and Fox 1999).

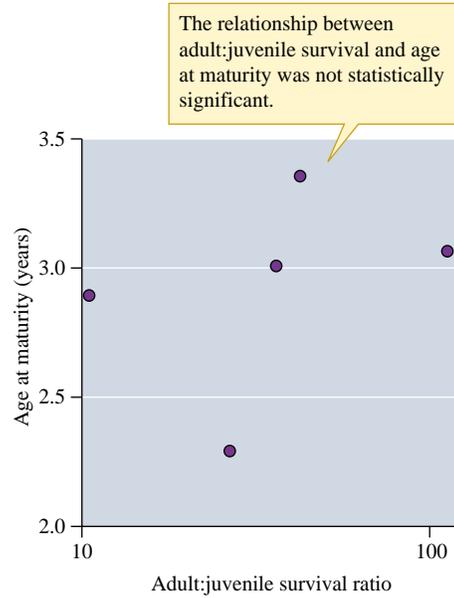


FIGURE 12.17 Adult:juvenile survival ratios and age at reproductive maturity in populations of pumpkinseed sunfish (data from Bertschy and Fox 1999).

CASE HISTORIES: life history classification



The great diversity of life histories may be classified on the basis of a few population characteristics, such as fecundity or number of offspring, m_x , survival, l_x , and age at reproductive maturity, α .

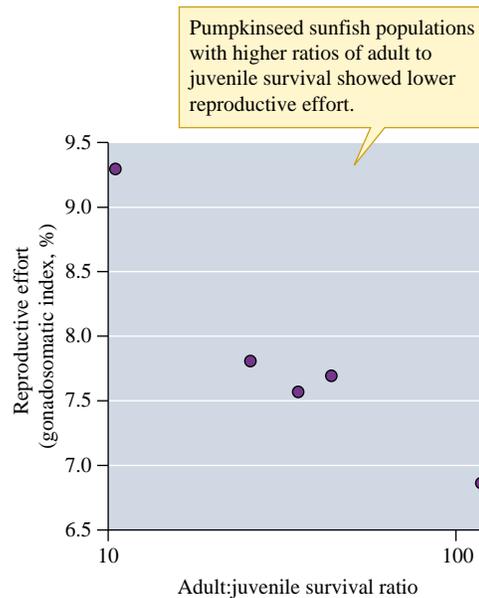


FIGURE 12.18 Adult:juvenile survival ratio and reproductive effort as measured by the gonadosomatic index or GSI (data from Bertschy and Fox 1999).

While classification systems never capture the full diversity of nature, they make working with the often bewildering variety of nature much easier. It is important to bear in mind when using classification systems, however, that they are an abstraction from nature and that most species fall somewhere in between the extreme types.

r and K selection

One of the earliest attempts to organize information on the great variety of life histories that occur among species was under the heading of r selection and K selection (MacArthur and Wilson 1967). The term **r selection**, which refers to the per capita rate of increase, r , which we calculated in chapter 10, was defined by Robert MacArthur and E. O. Wilson as selection favoring a higher population growth rate. MacArthur and Wilson suggested that r selection would be strongest in species often colonizing new or disturbed habitats. Therefore, high levels of disturbance would lead to ongoing r selection. MacArthur and Wilson contrasted r selected species with those subject mainly to K selection. The term **K selection** refers to the carrying capacity of the logistic growth equation summarized in figure 11.12. MacArthur and Wilson proposed that K selection favors more efficient utilization of resources such as food and nutrients. They envisioned that K selection would be most prominent in those situations where species populations are near carrying capacity much of the time.

Eric Pianka (1970, 1972) developed the concept of r and K selection further in two important papers. Pianka pointed out that r selection and K selection are the endpoints on a continuous distribution and that most organisms are subject to forms of selection somewhere in between these extremes. In addition, he correlated r and K selection with attributes of the environment and of populations. He also listed the population characteristics that each form of selection favors. Following MacArthur and Wilson, Pianka predicted that while r selection should be characteristic of variable or unpredictable environments, fairly constant or predictable environments should create conditions for K selection. In such conditions survivorship among r selected species will approximate type III, while K selected species should show type I or II survivorship (see fig. 10.6). Table 12.1 summarizes Pianka's proposed contrast in population characteristics favored by r versus K selection.

Pianka's detailed analysis clarified the sharp contrast between the two selective extremes represented by r and K selection by revealing biological details. The most fundamental contrasts are of course between intrinsic rate of increase, r_m , which should be highest in r selected species, and competitive ability, which should be highest among K selected species. In addition, according to Pianka, development should be rapid under r selection and relatively slow under K selection. Meanwhile, early reproduction and smaller body size will be favored by r selection, while K selection favors later reproduction and larger body size. Pianka predicted that reproduction under r selection will tend toward a single reproductive

Table 12.1
Characteristics favored by r versus K selection

Population attribute	r selection	K selection
Intrinsic rate of increase, r_m	High	Low
Competitive ability	Not strongly favored	Highly favored
Development	Rapid	Slow
Reproduction	Early	Late
Body size	Small	Large
Reproduction	Single, semelparity	Repeated, iteroparity
Offspring	Many, small	Few, large

(after Pianka 1970)

event in which many small offspring are produced. This type of reproduction, which is called **semelparity**, occurs in organisms such as annual weeds and salmon. In contrast, K selection should favor repeated reproduction, or **iteroparity**, of fewer larger offspring. Iteroparity, which spaces out reproduction over several reproductive periods during an organism's lifetime, is the type of reproduction seen in most perennial plants and most vertebrate animals. Pianka's contrast puts a name on and fleshes out the comparison we developed in chapter 11, where we contrasted organisms that are "small and fast," analogous to r selected species, with ones that are "large and slow," analogous to K selected species (fig. 12.19).

The ideas of r and K selection helped greatly as ecologists and evolutionary biologists attempted to think more systematically about life history variation and its evolution. However, ecologists who found that the dichotomy of r versus K did not include a great deal of known variation in life histories have proposed alternative classifications.

Plant Life Histories

J. P. Grime (1977, 1979) proposed that variation in environmental conditions has led to the development of distinctive strategies or life histories among plants. The two variables that he selected as most important in exerting selective pressure on plants were the intensity of disturbance and the intensity of stress. Grime contrasted four extreme environmental types which he characterized by combinations of disturbance intensity and stress intensity. Four environmental extremes envisioned by Grime were: (1) low disturbance–low stress, (2) low disturbance–high stress, (3) high disturbance–low stress, and (4) high disturbance–high stress. Drawing on his extensive knowledge of plant biology, Grime suggested that plants occupy three of his theoretical environments but that there is no viable strategy among plants for the fourth environmental combination, high disturbance–high stress.



FIGURE 12.19 Mouse and elephant, *r* selection versus *K* selection?

Grime next described plant strategies, or life histories, that match the requirements of the remaining three environments. His strategies were ruderal, stress-tolerant, and competitive (fig. 12.20). **Ruderal**s are plants that live in highly disturbed habitats and that may depend on disturbance to persist in the face of potential competition from other plants. Grime summarized several characteristics of ruderal plants that allow them to persist in habitats experiencing frequent and intense **disturbance**, which he defined as any mechanisms or processes that limit plants by destroying plant biomass. One of the characteristics of ruderal plants is their capacity to grow rapidly and produce seeds during relatively short periods between successive disturbances. This capacity alone would favor persistence of ruderal plants in the face of frequent disturbance. In addition, however, ruderal plants also invest a large proportion of their biomass in reproduction, producing large numbers of seeds that are capable of dispersing to new habitats made available by disturbance. The term ruderal is sometimes used synonymously with the term “weed.” Animals that are associated with disturbance, have high reproductive rates, and are good colonists, are also sometimes referred to as ruderal.

Grime (1977) began his discussion of the second type of plant life history, stress-tolerant, with a definition of

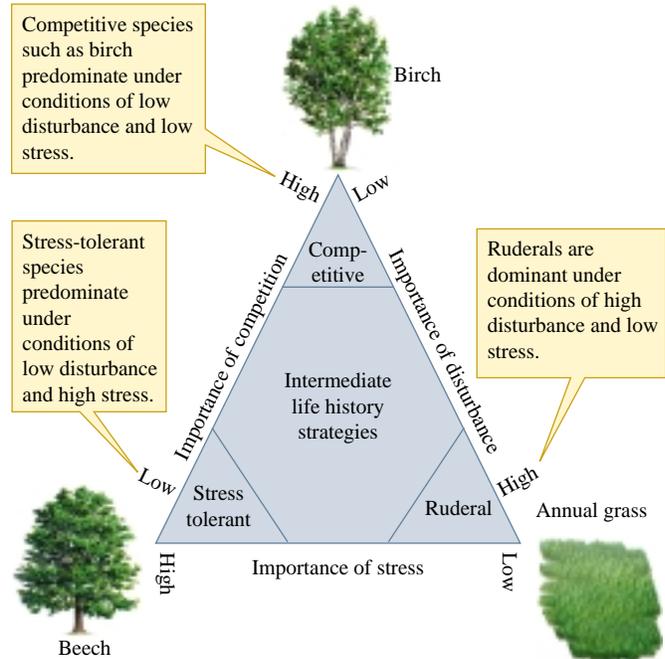


FIGURE 12.20 Grime's classification of plant life history strategies (after Grime 1979).

stress as “. . . external constraints which limit the rate of dry matter production of all or part of the vegetation.” In other words, stress is induced by environmental conditions that limit the growth of all or part of the vegetation. What environmental conditions might create such constraints? Our discussions in chapters 4, 5, and 6, where we considered temperature, water, and energy and nutrient relations, provide several suggestions. Stress is the result of extreme temperatures, high or low, extreme hydrologic conditions, too little or too much water, or too much or too little light or nutrients. Because different species are adapted to different environmental conditions, the absolute levels of light, water, temperature, and so forth that constitute stress will vary from species to species. In addition, conditions that induce stress will vary from biome to biome. For instance, the amount of precipitation leading to drought stress is different in rain forest and desert, or the minimum temperatures inducing thermal stress are different in tropical forest compared to boreal forest.

The important point that Grime made, however, was that in every biome, some species are more tolerant to the environmental extremes that occur. These are the species that he referred to as “stress-tolerant.” **Stress-tolerant plants** are those that live under conditions of high stress but low disturbance. Grime proposed that, in general, stress-tolerant plants grow slowly, are evergreen, conserve fixed carbon, nutrients, and water, and are adept at exploiting temporary favorable conditions. In addition, stress-tolerant plants are often unpalatable to most herbivores. Because stress-tolerant species endure some of the most difficult conditions a particular environment has to offer, they are

there to take advantage of infrequent favorable periods for growth and reproduction.

The third plant strategy proposed by Grime, the competitive strategy, is in many respects intermediate between the ruderal strategy and the stress-tolerant strategy. In Grime's classification **competitive plants** occupy environments where disturbance intensity is low and the intensity of stress is also low. Under conditions of low stress and low disturbance, plants have the potential to grow well. As they do so, however, they eventually compete with each other for resources, such as light, water, nutrients, and space. Grime's model predicts that the plants living under such circumstances will be selected for strong competitive abilities.

How does Grime's system of classification compare with the r and K selection contrast proposed by MacArthur and Wilson and Pianka? Grime proposed that r selection corresponds to his ruderal strategy or life history, while K selection corresponds to the stress-tolerant end of his classification. Meanwhile, he placed the competitive life history category in a position intermediate between the extremes represented by r selection and K selection. However, while attempting this reconciliation of the two classifications, Grime suggested that a linear arrangement of life histories with r selection and K selection occupying the extremes fails to capture the full variation shown by organisms. He suggested that more dimensions are needed and, of course, Grime's triangular arrangement (fig. 12.20) adds another dimension. The factors varying along the edges of Grime's

triangle are intensity of disturbance, stress, and competition. Other ecologists have also recognized the need for more dimensions in representing life history diversity.

Opportunistic, Equilibrium, and Periodic Life Histories

In a review of life history patterns among fish, Kirk Winemiller and Kenneth Rose (1992) proposed a classification of life histories based on some of the aspects of population dynamics that we reviewed in chapter 10. They drew particular attention to survivorship especially among juveniles, l_x , fecundity or number of offspring produced, m_x , and generation time or age at maturity, α . Table 10.2 summarized the relationship between these variables. While the analysis by Winemiller and Rose overlaps those of Pianka and Grime, their system adds coherence to life history classification by its linkage to fundamental elements of population ecology, l_x , m_x , and α .

Winemiller and Rose start, as we began chapter 12, with the concept of trade-offs. Their trade-offs are among fecundity, survivorship, and age at reproductive maturity. Using variation in fish life histories as a model, Winemiller and Rose proposed that life histories should lie on a semitriangular surface as shown in figure 12.21. They called the three endpoints on their surface "opportunistic," "equilibrium," and "periodic" life histories. The opportunistic strategy, by combining

low juvenile survival, low numbers of offspring, and early reproductive maturity, maximizes colonizing ability across environments that vary unpredictably in time or space. It is important to keep in mind, however, that while the absolute reproductive output of opportunistic species may be low, the percentage of their energy budget allocated to reproduction is high. Winemiller and Rose's equilibrium strategy combines high juvenile survival, low numbers of offspring, and late reproductive maturity. Finally, the periodic strategy combines low juvenile survival, high numbers of offspring, and late age at maturity. Among fish, periodic species tend to be large and produce numerous small offspring. By producing large numbers of offspring over a long life span, periodic species can take advantage of infrequent periods when conditions are favorable for reproduction.

It is difficult to map the exact correspondence of Winemiller and Rose's classification of life history

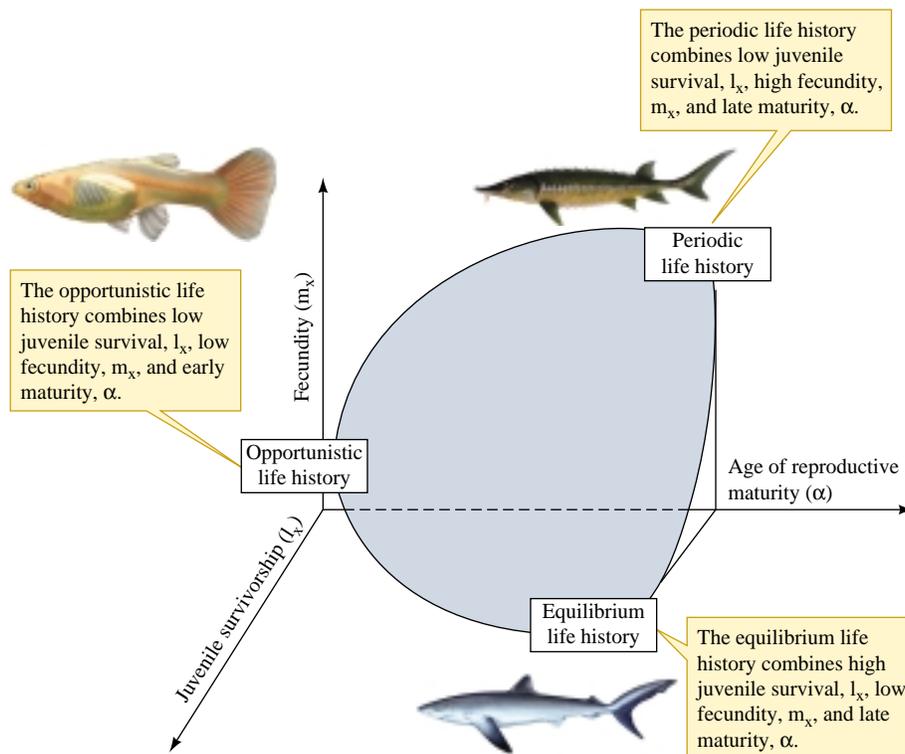


FIGURE 12.21 Classification of life histories based on juvenile survival, l_x , fecundity, m_x , and age at reproductive maturity, T (after Winemiller and Rose 1992a).

strategies to either the r-K continuum of MacArthur and Wilson and Pianka or the triangular classification of plant life histories developed by Grime. For instance, opportunistic species share characteristics with r selected and ruderal species. However, opportunistic species differ from the typical r selected species because they tend to produce small clutches of offspring. The equilibrium strategy, which combines production of high juvenile survival, low numbers of offspring, and late reproductive maturity, approaches the characteristics of typical K selected species. Winemiller and Rose point out, however, that many fish classified as “equilibrium” are small, while typically K selected species tend toward large body size (see table 12.1). Periodic species are not captured by the linear r to K selection gradient. Meanwhile the periodic and equilibrium species in Winemiller and Rose’s classification share some characteristics with Grime’s stress-tolerant and competitive species but differ in other characteristics.

In this review of systems for life history classification, we have focused on just three of the many that have been proposed. Even with just these three, however, translation from one classification to another is difficult. What are the sources of these differences in perspective? One of the sources is that different ecologists have worked with different groups of organisms. While MacArthur and Wilson’s system was built after years of work on birds and insects, respectively, Pianka had worked mainly with lizards. Grime’s classification was

built on and intended for plants. Finally, the perspective of Winemiller and Rose was influenced substantially by their work with fish. Because these ecologists worked with such different groups of organisms, it is not surprising that their classifications of life histories do not overlay precisely.

However, it may be that the analysis by Winemiller and Rose has laid the foundation for a more general theory of life histories. By basing their classification system on some of the most basic aspects of population ecology, l_x , m_x , and α , Winemiller and Rose (1992a) established a common currency for representing and analyzing life history information for any organism. As a model for how such a translation might be done, Winemiller and Rose (1992b) plotted the distributions of life history parameters of representative animal groups on their life history classification axes (fig. 12.22). By plotting life history variation among vertebrate groups on the same axes using the same variables, figure 12.22 demonstrates differences in the amount of life history variation between the groups. Notice that fish show the greatest variation and mammals the least, while birds and reptiles and amphibians include intermediate levels of variation.

The knowledge of species life histories revealed by the studies of life history ecologists has produced a subdiscipline of ecology rich in both theory and biological detail. In the challenges that lie ahead as we work to conserve endangered species, both theory and detailed knowledge of the life histories

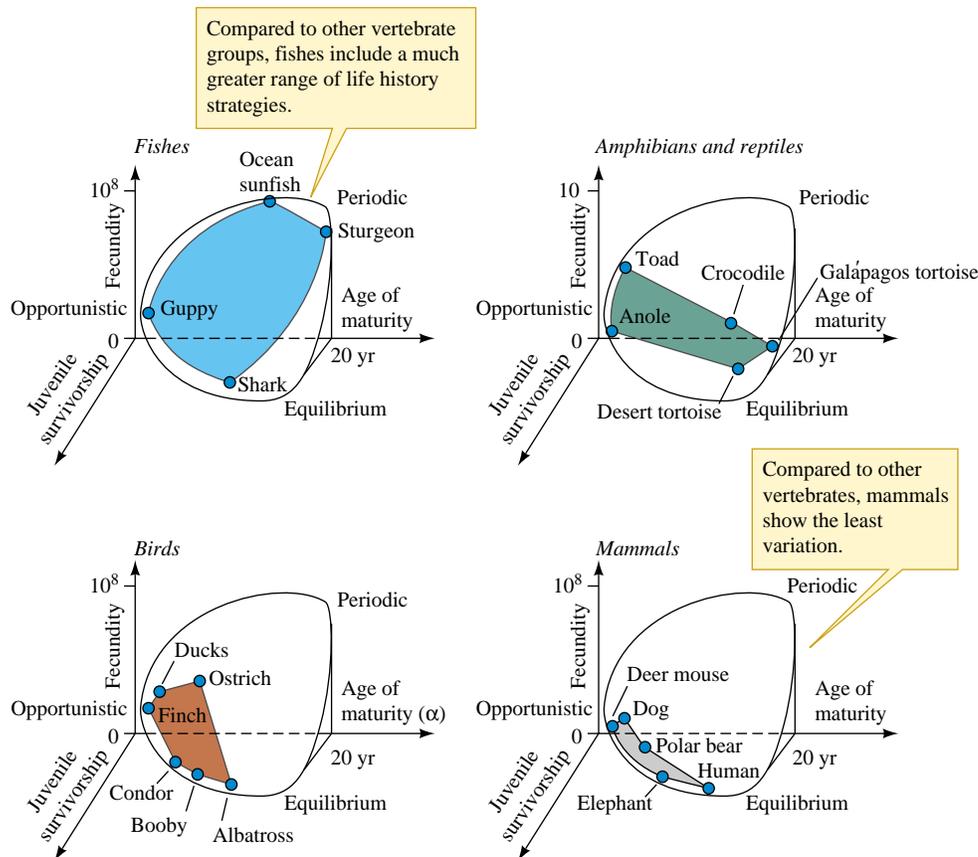


FIGURE 12.22 Variation in life histories within vertebrate animals (after Winemiller and Rose 1992b).

of individual species will be important. For instance, life history information is playing a key role in the conservation of riparian forests across western North America.

APPLICATIONS AND TOOLS: using life history information to restore riparian forests

Riparian ecosystems all over the planet are threatened by human modification of rivers. Impacts on these ecosystems come from a variety of sources, including channelizing of rivers, damming to control flooding, and diverting water for agricultural and urban uses. These modifications have greatly reduced the natural complexity of riverine landscapes and have eliminated the natural flow regime on most rivers. The effects of these modifications on landscape structure and processes within riparian zones are discussed in the Applications and Tools section of chapter 21. Here we consider how these modifications impact key tree species in riparian forests and how ecologists are using their understanding of life histories to restore those forests.

As we saw in chapter 3, riparian zones are transitions between the aquatic environment of the river and the upland

terrestrial environment. Because they inhabit this transition zone, riparian organisms are adapted to periodic flooding. However, many riparian species not only tolerate flooding but many require it to remain healthy and complete their life cycles. Some the organisms most dependent on the natural cycle of flooding and drying in riparian zones are the trees that form the dominant structure of riparian ecosystems.

Riparian forests support large numbers of species and high population densities of many species, particularly in arid and semiarid lands (fig. 12.23). Many species of trees inhabit riparian zones at middle latitudes and while the number and kinds of species changes from one region to another, two of the most common riparian trees are willows, *Salix* spp., and cottonwoods, *Populus* spp., both of which depend on flooding to maintain their populations. In western North America, cottonwood-willow riparian forests support a very large proportion of the diversity of the region, particularly among birds, reptiles, amphibians, and invertebrates such as butterflies and ground beetles. Riparian forests also provide critical wintering grounds for populations of large vertebrates such as elk, or wapiti, in the northern regions of the west. During the past century over 90% of riparian forests have been lost across western North America and much of the rest is threatened.

Jeff Braatne, Stewart Rood, and P. E. Heilman (1996) listed 10 major impacts of human activity on cottonwood-willow



FIGURE 12.23 Cottonwood riparian forest: an island of green and diversity in semi-arid landscapes.

riparian forests in western North America. One of the chief threats to the riparian forests of the region results from the building of dams and subsequent flow control and diversion of water for irrigation. The negative impact of dams on cottonwoods in western North America has been well documented. Braatne, Rood, and Heilman's list of impacts of dams on cottonwoods include reduced growth by established cottonwood trees, lower cottonwood abundance, increased mortality, altered growth form, and reduced germination and seedling establishment. These impacts are mainly the result of four environmental changes induced by dams and river management: reduced water availability, reduced flooding, stabilized flows, and simplified river channel structure.

Of the many potential effects of dams and their management on riparian cottonwoods, one of the most critical is their negative impact on seed germination and seedling establishment. Without the establishment of young cottonwoods, the entire riparian forest will eventually die and the diversity of organisms that the forest supports will be lost. Can flows from dams be managed to prevent flood damage to property and loss of human life and still maintain cottonwood riparian forests? This is a question addressed by the work of John Mahoney of Alberta Environment Protection, Alberta, Canada, and Stewart Rood of the University of Lethbridge, Alberta, Canada. A key to the success of the work by Mahoney and Rood (1998) is an intimate knowledge of the life history of cottonwood trees.

As we saw in chapter 10 (fig. 10.8), flood control on the Rio Grande in New Mexico has largely eliminated reproduction by Rio Grande cottonwood trees, *Populus deltoides* subsp. *wislizenii*. Like other cottonwood species, the Rio Grande cottonwood requires flooding to prepare a seed bed of moist bare soil in which its seeds can germinate and its young trees become established. In addition to preparing the seed bed, floods are also critical for keeping soils moist long enough for the roots of young cottonwood trees to grow into the shallow groundwater of riparian zones.

With this background in mind, Mahoney and Rood built a model for flow management by dams that would foster, rather than inhibit, cottonwood germination and establishment (fig. 12.24). The first step in their analysis was to describe the **phenology** of cottonwood trees. Phenology is the study of the relationship between climate and the timing of ecological events such as the date of arrival of migratory birds on their wintering grounds or the timing of spring plankton blooms. In the case of cottonwoods, Mahoney and Rood

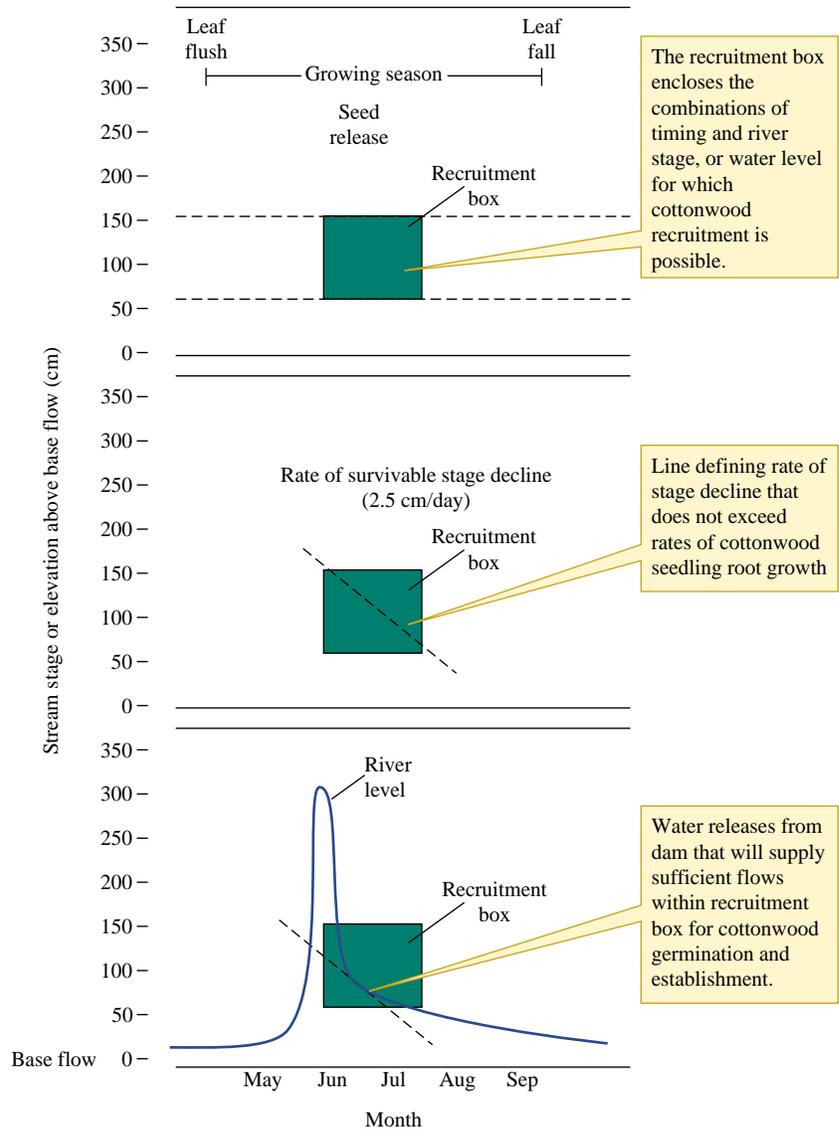


FIGURE 12.24 River management to sustain cottonwood riparian forests (after Mahoney and Rood 1998).

bounded the growing season with cottonwood leaf flush to mark the beginning of the growing season and with leaf fall to mark its end. Because their goal was to build a model that would predict the potential timing of cottonwood germination and seedling establishment, the most critical phenological event within the growing season was the timing of seed release by female cottonwood trees. The timing of river flows to foster cottonwood germination must coincide with the period when cottonwood trees are releasing their seed.

A second step in Mahoney and Rood's model building was to determine how much elevation of river level would be required to flood potential seedbeds for new cottonwood trees. Releases of water from the dam that did not flood these areas would produce no recruitment of young cottonwoods. The results of these first steps produced the "recruitment box" shown in figure 12.24.

Having established when flood flows should be released and what level or stage they should attain, Mahoney and Rood next turned to the maximum rate at which flows could be reduced by river managers and still promote cottonwood seedling establishment. They realized that germination is only one step on the way to successful seedling establishment. Because cottonwood seedlings in semiarid landscapes draw critical water from the shallow groundwater, flows must be drawn down at a rate that does not exceed the rate of seedling root growth. For young cottonwoods to successfully establish, flood waters must recede slowly enough so that the growth of the young cottonwood roots can keep pace. If flood waters fall too quickly, the roots of the young trees will not grow down to the groundwater level and they will die. Using results from their own experiments and the published results of other researchers, Mahoney and Rood proposed a survivable rate of river level, or stage, decline of 2.5 cm per day. This rate of stage decline is given by the middle panel in figure 12.24. The most important feature of this line is its slope. If the slope is much steeper than that shown in figure 12.24, Mahoney and Rood's data indicated that the rate of groundwater-level fall will exceed the rate of root growth by cottonwood seedlings.

The next stage in the analysis was to specify flow releases that would be workable within existing programs of river management and produce needed cottonwood reproduction. Throughout the intermountain region of western North America where Mahoney and Rood worked on their model, peak flows occur in late spring and then gradually decline into late summer when they approach base flows. Cottonwood seed release across

much of western North America extends from May into July, coinciding with peak flows across the region. Two factors were critical in their recommendations to river managers. First, ensuring that peak flows overlap with the "recruitment box" in the model and second, making sure that high spring flows recede at a rate that does not exceed the rate of seedling root growth. That rate is given by the dashed line in the lower panel of figure 12.24. Mahoney and Rood point out that to maintain this slope during draw down, the flow peak which precedes the recruitment box must exceed the height of the recruitment box. Lower peak flows will be followed by a drop in groundwater level that is too rapid to allow cottonwood establishment.

Mahoney and Rood's recruitment box model has the potential to help conserve and sustain cottonwood riparian forest in western North America and with modification could be applied to very different riparian ecosystems. Preliminary indications are that following the recommendations of the model can lead to successful cottonwood recruitment. Managers following recommendations of the model have stimulated successful recruitment of cottonwood seedlings along the Oldman River in Alberta, Canada, and along the Truckee River near Reno, Nevada. Experiments and experiences such as these provide models for collaboration between ecologists, conservationists, and natural resource managers. However, as Mahoney and Rood point out, these exercises also improve our understanding of basic ecological processes such as basic cottonwood reproductive ecology. Improved understanding of basic ecology will in turn make any management programs directed at the species even more successful.



SUMMARY CONCEPTS

Life history consists of the adaptations of an organism that influence aspects of their biology such as the number of offspring it produces, its survival, and its size and age at reproductive maturity. This chapter presents case histories bearing on some of the central concepts of life history ecology.

Because all organisms have access to limited energy and other resources, there is a trade-off between the number and size of offspring; those that produce larger offspring are constrained to produce fewer, while those that produce smaller offspring may produce larger numbers. Turner and Trexler found that larger darter species produce larger numbers of eggs. Their results also support the generalization that there is a trade-off between offspring size and number. On average, darters that produce larger eggs produce few eggs. They found a strong positive relationship between gene flow among darter populations and the number of eggs produced by females and a negative relationship between egg size and gene flow. Plant ecologists have also found a negative relationship between sizes

of seeds produced by plants and the number of seeds they produce. Westoby, Leishman, and Lord found that plants of different growth form and different seed dispersal mechanisms tend to produce seeds of different sizes. Larger seeds, on average, produce larger seedlings that have a higher probability of successfully recruiting, particularly in the face of environmental challenges such as shade and competition.

Where adult survival is lower, organisms begin reproducing at an earlier age and invest a greater proportion of their energy budget into reproduction; where adult survival is higher, organisms defer reproduction to a later age and allocate a smaller proportion of their resources to reproduction. Shine and Charnov found that as survival of adult lizards and snakes increases, their age at maturity also increases. Gunderson found analogous patterns among fish. In addition, fish with higher rates of mortality allocate a greater proportion of their biomass to reproduction. In other words, they show higher reproductive effort. These generalizations

are supported by comparisons both between and within species. For instance, pumpkinseed sunfish allocate greater energy, or biomass, to reproductive effort where adult pumpkinseed survival is lower.

The great diversity of life histories may be classified on the basis of a few population characteristics, such as number of offspring, m_x , survival, l_x , and age at reproductive maturity, α . One of the earliest attempts to organize information on the great variety of life histories that occur among species was under the heading of r selection and K selection. r selection refers to the per capita rate of increase, r , and is thought to favor higher population growth rate. r selection is predicted to be strongest in disturbed habitats. K selection refers to the carrying capacity in the logistic growth equation and is envisioned as a form of natural selection favoring more efficient utilization of resources such as food and nutrients. Grime described plant strategies, or life histories, that match the requirements of three environments:

(1) low disturbance–low stress, (2) low disturbance–high stress, (3) high disturbance–low stress. His plant strategies matching these environmental conditions were competitive, stress-tolerant, and ruderal. Based on life history patterns among fish, Kirk Winemiller and Kenneth Rose proposed a classification of life histories based on survivorship especially among juveniles, l_x , fecundity or number of offspring produced, m_x , and generation time or age at maturity, α . By basing their classification system on some of the most basic aspects of population ecology, l_x , m_x , and α , Winemiller and Rose established a common currency for representing and analyzing life history information for any organism.

Life history information is playing a key role in the conservation of riparian forests across western North America. As ecologists contribute to the management of endangered populations, they also increase our understanding of basic population ecology.

REVIEW QUESTIONS

- The discussion on seed size and number focused mainly on the advantages associated with large seeds. However, research by Westoby, Leishman, and Lord has revealed that the plants from widely separated geographic regions produce a wide variety of seed sizes. If this variation is to be maintained, what are some of the advantages associated with producing small seeds?
- Under what conditions should natural selection favor production of many small offspring versus the production of a few well provisioned offspring?
- Plant ecologists using experimental studies have verified that seedlings growing from larger seeds have a better chance of surviving environmental challenges such as deep shade, drought, physical injury, and competition from other plants. Explain how growing from larger seeds could give an advantage to seedlings facing strong environmental challenge to their establishing.
- The studies by Shine and Charnov (1992) and Gunderson (1997) addressed important questions of concern to life history ecologists and their work provided robust answers to those questions. However, the methods they employed differed substantially from those used in most of the studies discussed in this and other chapters. The chief difference is that both relied heavily on data on life histories published previously by other authors. What was it about the nature of the problems addressed by these authors that constrained them to use this approach? In what sorts of study would it be most appropriate to perform a synthesis of previously published information?
- Much of our discussion of life history variation involved variation among species within groups as broadly defined as “fish,” “plants,” or “reptiles.” However, the work of Bertschy and Fox revealed significant variation in life history within species. In general, what should be the relative amount of variation within a species compared to that among many species? Develop your discussion using relative amounts of genetic variation upon which natural selection might act. You might review the sections discussing the evolutionary significance of genetic variation in chapter 8.
- Grime’s proposed classification of environments based on intensity of disturbance and stress resulted in four environments, three of which he proposed were inhabitable by plants and one of which was not. That fourth environment shows high intensity of disturbance and high stress. What sorts of life histories would an organism have to possess to live in such an environment? What kinds of real organisms can you think of that could live and perhaps thrive in such an environment. (Hint: Look for some ideas in figs. 10.11 and 11.21)?
- Once established, Rio Grande cottonwoods can live to be well over 100 years old. However, they experience very high rates of mortality as seeds, which only germinate in conditions that occur very unpredictably in time and space. Female cottonwood trees produce about 25 million seeds annually and could produce up to two and a half billion seeds during a life time. Which of the life history categories that we’ve discussed most closely match the life history of the Rio Grande cottonwood.
- Using what you know about the trade-off between seed number and seed size (e.g., fig. 12.7) and patterns of variation among plants, predict the relative number of seeds produced by the various plant growth forms and dispersal strategies listed on figure 12.8.
- Apply Winemiller and Rose’s model to plants. If you were to construct a strictly quantitative classification of plant life histories using Winemiller and Rose’s approach, what information would you need about the plants included in your analysis? How many plant species would you need to have an idea of how variation in their life histories compares with those of animals (e.g., as in fig. 12.22)? Try to reconcile Grime’s plant classification with the scheme offered by Winemiller and Rose. Where are they similar? How are they different?
- Suppose you are a river manager and you need to operate the dams on your river in a way that fosters riparian tree growth. However, assume that the dominant trees along the river that you manage are not cottonwoods. In order to apply Mahoney and Rood’s recruitment box model, what information do you need to know about your river and the riparian tree species you intend to manage? How would you go about gathering this information?

SUGGESTED READINGS

- Bertschy, K. A. and M. G. Fox. 1999. The influence of age-specific survivorship on pumpkinseed sunfish life histories. *Ecology* 80:2299–2313.
Interesting and well-designed study of variation in life histories between populations of the same species.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169–94.
- Grime, J. P. 1979. *Plant Strategies and Vegetation Processes*. New York: John Wiley & Sons.
Classical publications on plant life histories. These two publications provide a foundation for understanding plant life histories.
- Jakobsson, A. and O. Eriksson. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos* 88:494–502.
This paper provides an entry into modern experimental research on plant life histories.
- Mahoney, J. M. and S. B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment—an integrative model. *Wetlands* 18:634–45.
Excellent exposition of the application of life history ecology to the solution of a significant environmental problem.
- Roff, D. A. 1993. *The Evolution of Life Histories: Theory and Analysis*. New York: Chapman & Hall.
- Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.
Two texts that give broad introductions to the evolution of life histories.
- Tracy, C. R. 1999. Differences in body size among chuckwalla (*Sauromalus obesus*) populations. *Ecology* 80:259–71.
A complement to the paper by Jakobsson and Eriksson that provides insights into approaches used by animal ecologists.
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