**Learning Objectives**

- Clarify the relationship between population growth rate, birth rate, and death rate.
- Compare trade-offs between survival and reproduction for altricial species to those of precocial and nest parasite species.
- Describe the relationship between age at maturity and growth rate.
- Analyze the equation for population growth rate.
- Describe several means of dispersal, and its importance to population density.

What happens when births exceed deaths?

Obviously a population grows. For some populations this is necessary to ensure the survival of the species. For other species this can cause some serious issues.

**Births and Deaths**

**Balancing Costs of Reproduction and Survival**

The **growth rate** of a population is the change in population size per member of the population per unit of time. The symbol \( r \) denotes growth rate. Growth rate clearly depends on **birth rate** \( b \), the number of births per individual within the population per unit of time, as well a **death rate** \( d \), the number of deaths per individual per unit of time. The following equation calculates growth rate, according to our preliminary understanding:

\[
r = b - d
\]

growth rate = birth rate - death rate

If birth rate exceeds death rate, \( r \) is positive and the population grows. If death rate exceeds birth rate, \( r \) is negative and the population declines. And if birth rate and death rate are in equilibrium, growth rate is zero, and the population remains stable. In a stable population, each individual, on the average, produces one offspring which survives
long enough to reproduce itself. Mere survival is not success in the game of life; natural selection requires that survivors reproduce. As Malthus realized, nearly all species have the potential to grow - to reproduce many more than just a single replacement offspring. However, species vary in the strategies they use to achieve reproductive success, making trade-offs between the energy and time “costs” of survival and those of reproduction. Age at first reproduction, frequency of reproduction, number of offspring, parental care, reproductive lifespan, and offspring death rate are some of the traits which build strategies for successful reproduction.

Analyzing extreme examples can help you understand the trade-offs species must make between survival and reproductive success. Let’s compare two groups of birds. Somewhat like precocious children who mature early, precocial birds run around to find their own food soon after hatching. Geese, ducks, and chickens use this strategy for raising their young (Figure 1.2). Often living and nesting on the ground, precocial species are subject to high predation rates, so few survive long enough to reproduce. Therefore, those who do reproduce lay many eggs at once, and these eggs are large. The young emerge well-developed, ready to feed and escape predators soon after hatching. Precocial species invest a great deal of energy in a large number of offspring but do not spend much energy on parental care, because even though some offspring are likely to die, others will survive long enough to reproduce.

Contrast this precocial strategy with the opposite, altricial strategy used by robins and hummingbirds (Figure 1.3). These birds hatch helpless and naked, completely unprepared for independent life. Parents invest little energy in just a few, small eggs; hummingbirds’ eggs are the smallest in the bird world, and average two per nest. However, survival of these offspring matters a great deal, because there are so few. So, parents build elaborate nests safely hidden in trees and invest a great deal of energy hunting for food around-the-clock until the young have developed enough to fledge and find food on their own.

Precocial and altricial birds play by the rules of costs and benefits, each group using a different strategy. Cowbirds, however, make up their own rules, earning them the title of “parasites” in the bird world. How can a bird be a parasite? Cowbirds are altricial, but they parasitize by laying their eggs in other birds’ nests, thereby escaping the high costs of parental care (Figure 1.4). Cowbird eggs are usually slightly larger and hatch a little sooner than the host eggs affording cowbird parents a bit of extra energy. “Early bird” hatchlings do indeed “get the worm,” easily out-competing their smaller host siblings for parental food deliveries. Sometimes, they are strong enough to ungratefully oust their “sibs” from the nest. On the other hand, host parents occasionally recognize and eject the foreign egg before it hatches. Yellow warblers simply block off the offending egg (along with their own eggs) by building a new nest bottom. They then lay a new clutch of their own eggs (The eggs are not their primary energy investment). A five-“story” nest holds the record for yellow warbler (and cowbird?) determination!

Many species fall in between the extremes of precocial and altricial strategies, but all must make trade-offs between the costs of reproduction and those of surviving predation, competition, and disease, in order to ensure that at least one offspring per adult survives long enough to reproduce. It’s worth reprising the survivorship curves introduced in the previous lesson to illustrate these trade-offs (Figure 1.5). Which curve illustrates the precocial strategy used by
FIGURE 1.3
Hummingbirds illustrate an **altricial** reproductive strategy. Very little energy is spent to produce two tiny eggs, but they are enclosed in a secluded nest, usually hidden in a tree. Survival of the offspring is critical because there are only two, so parents invest tremendous amounts of energy finding food for themselves and their young for nearly three weeks. This energy investment allows the offspring to develop to nearly adult size before they fledge into the world of predators and competition.

FIGURE 1.4
A Brown-headed Cowbird egg in an Eastern Phoebe’s nest illustrates yet another strategy for reproductive success: invest all of your energy in a single egg, just large enough to out-compete your altricial host’s eggs, and let the host parents feed your offspring! The right photo shows a male individual of this parasitic species.

ducks, chickens, and grouse? Which curve demonstrates the altricial strategy of robins and hummingbirds? What shape do you think a cowbird’s survivorship curve might take?

FIGURE 1.5
Survivorship curves show the various strategies for achieving population growth by adjustments in birth rate and death rate. Recall that \( r = b - d \). Hummingbirds have low birth rates \( (b) \), but through time and energy spent on parental care and feeding, ensure high survival rates for their altricial offspring (low \( d \)). Geese, however, invest energy in many large eggs (high \( b \)) to offset high death rates from predation (\( d \)) among their precocial offspring.
One more strategy involves variation of age at maturity. All other factors being equal (number and size of offspring, survival rates, and more), delayed reproduction lowers population growth rate. Bald eagles require five years of growth before they are able to reproduce. If they were to lay the same number of eggs during their first year, those first-year offspring and several generations of *their* offspring, as well as the parents, would be able to reproduce during that time, tremendously increasing the overall population. By delaying reproduction, bald eagles not only ensure good energy supplies for reproduction at maturity, but also limit population density to suit their large bodied, long-lived life history.

**Summary**

- If birth rate (plus immigration) exceeds death rate (plus emigration), a population grows. If death rate exceeds birth rate, the population declines. And if birth rate and death rate are in equilibrium, growth rate is zero and the population remains stable.
- In a stable population, each individual (on the average) produces one offspring which survives long enough to reproduce itself.
- Altricial species have a few undeveloped offspring but invest a great deal of energy in parental care. Precocial species invest energy in a large number of well-developed offspring, but little in parental care.
- The earlier species begin to reproduce, the faster their population grows, with all other factors being equal.

**Review**

1. Summarize the equation for population growth rate, and explain each factor.
2. Compare survival and reproduction in altricial species to the same factors for precocial species.
3. How might delaying age of childbirth prevent the need to limit family size?

**References**

1. woodleywonderworks. [https://www.flickr.com/photos/wwwworks/2971831776](https://www.flickr.com/photos/wwwworks/2971831776) . CC BY 2.0