POPULATION ECOLOGY

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r-SELECTED STRATEGY OF POPULATION:

Populations often can be divided into one of two extreme types based on their life history strategy. Some populations,called *r*-selected, are considered opportunistic because their reproductive behaviour involves a high intrinsic rate of growth (*r*)—individuals give birth once at an early age to many offspring. Populations that exhibit this strategy often have been shaped by an extremely variable and uncertain environment. Because mortality occurs randomly in this setting, quantity of progeny rather than quality of care serves the species better.

K-SELECTED STRATEGIES OF POPULATION:

In another strategy, called *K*-selected, populations tend to remain near the carrying capacity (*K*), the maximum number of individuals that the environment can sustain. Individuals in a *K*-selected population give birth at a later age to fewer offspring. This equilibrial life history is exhibited in more stable environments where reproductive success depends more on the fitness of the offspring than on their numbers.

***Fig:K*-selected species**Adult and young African savanna elephants (*Loxodonta africana*) crossing a stream. Elephants are classic examples of *K*-selected species—that is, species characterized by relatively stable populations. Such species produce a few large young instead of many small young.

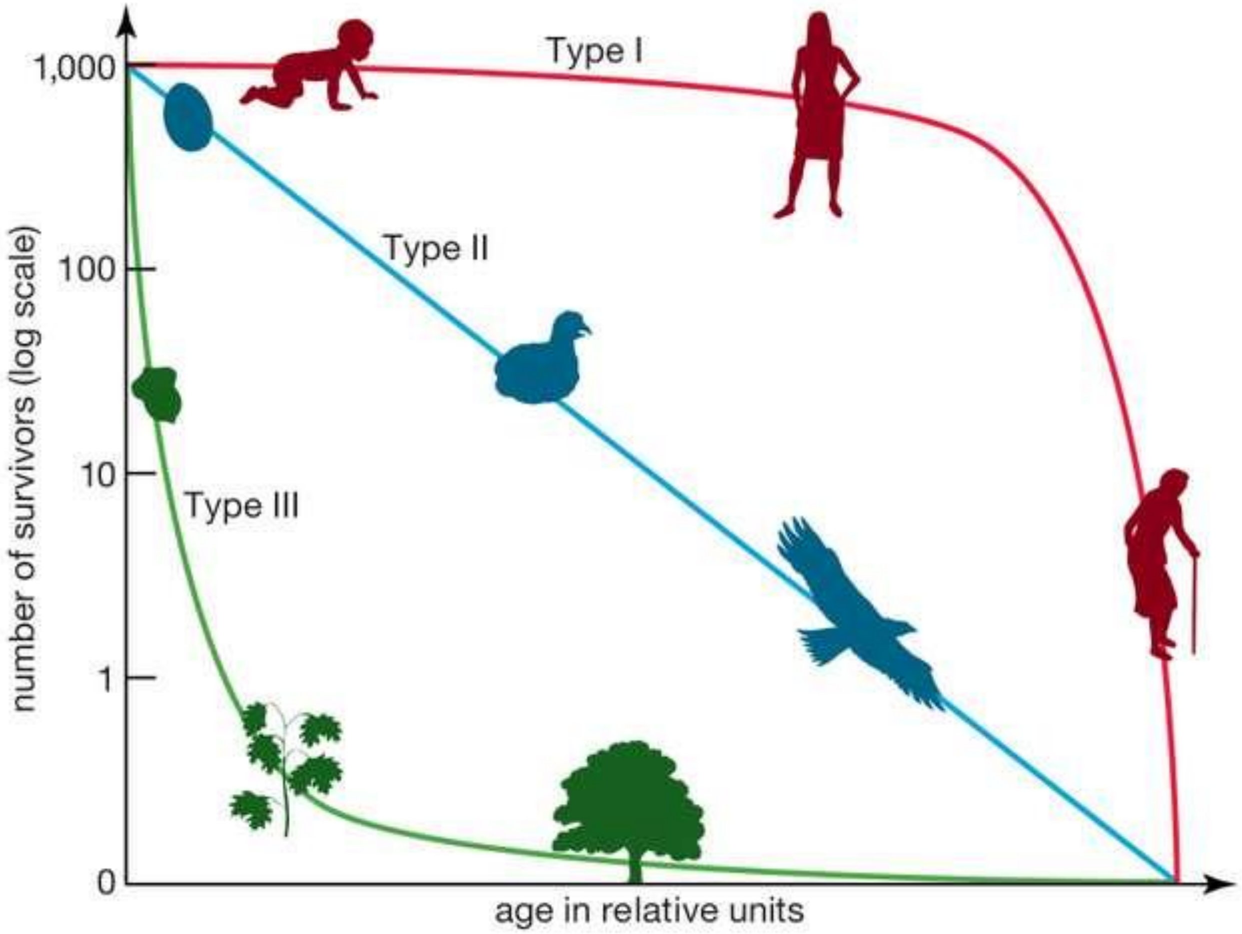
Life tables and the rate of population growth:

Differences in life history strategies, which include an organism's allocation of its time and resources to reproduction and care of offspring, greatly affect population dynamics. As stated above, populations in which individuals reproduce at an early age have the potential to grow much faster than populations in which individuals reproduce later. The effect of the age of first reproduction on population growth can be seen in the life tables for a particular species. Life tables were originally developed by insurance companies to provide a means of determining how long a person of a particular age could be expected to live. They are used not only by demographers of human populations but also by plant, animal, and microbial ecologists to make projections about the life expectancies of nonhuman populations, as well as the effects of variation on demography and population growth. The number of individuals in a closed population (a population in which neither immigration nor emigration occurs) is governed by the rates of birth (natality), growth, reproduction, and death (mortality). Life tables are designed to evaluate how these rates influence the overall growth rate of a population.

Survivorship curves:

Life tables follow the fate of a group of individuals all born within the same population in the same year. Of this group, or cohort, only a certain number of individuals will reach each age, and there is an age above which no individuals ever survive. Plotting the number of those members of the group that are still alive at each age results in a survivorship curve for the population.

Survivorship curves are usually displayed on a semi logarithmic rather than an arithmetic scale.



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survivorship curve Type I, II, and III survivorship curves.

A survivorship curve: is the graphic representation of the number of individuals in a population that can be expected to survive to any specific age.

Types:

TYPE-I:There are three general types of survivorship curves. Species such as humans and other large mammals, which have fewer numbers of offspring but invest much time and energy in caring for their young (*K*-selected species), usually have a Type I survivorship curve. This relatively flat curve reflects low juvenile mortality, with most individuals living to old age.

TYPE-II: A constant probability of dying at any age, shown by the Type II survivorship curve, is evident as a straight line with a constant slope that decreases over time toward zero. Certain lizards, perching birds, and rodents exhibit this type of survivorship curve. In some species that produce many offspring but provide little care for them (*r*-selected species), mortality is greatest among the youngest individuals.

Type III survivorship curve: indicative of this life history is initially very steep, which is reflective of very high mortality among the young, but flattens out as those individuals who reach maturity survive for a relatively longer time; it is exhibited by animals such as many insects or shellfish. Many populations have survivorship patterns that are more complex than, or fall in between, these three idealized curves. For example, passerine birds (perching birds such as finches) commonly suffer high mortality during the first year of life and a lower, more constant rate of death in subsequent years.

Calculating population growth

Life tables also are used to study population growth. The average number of offspring left by a female at each age together with the proportion of individuals surviving to each age can be used to evaluate the rate at which the size of the population changes over time. These rates are used by demographers and population ecologists to estimate population growth and to evaluate the effects of conservation efforts on endangered species.

Fig:Galapagos cactus finch (*Geospiza scandens*).

It has such a high reproductive rate that the population can more than double in size each generation.

The average number of offspring that a female produces during her lifetime is called the net reproductive rate (R_0).

If all females survived to the oldest possible age for that population, the net reproductive rate would simply be the sum of the average number of offspring produced by females at each age. In real populations, however, some females die at every age. The net reproductive rate for a set cohort is obtained by multiplying the proportion of females surviving to each age (l_x) by the average number of offspring produced at each age (m_x) and then adding the products from all the age groups: $R_0 = \Sigma l_x m_x$.

A net reproductive rate of 1.0 indicates that a population is neither increasing nor decreasing but replacing its numbers exactly. This rate indicates population stability. Any number below 1.0 indicates a decrease in population, while any number above indicates an increase. For example, the net reproductive rate for the Galapagos cactus finch (*Geospiza scandens*) is 2.101, which means that the population can more than double its size each generation.

Life table for one Darwin finch, the Galapagos cactus finch (Geospiza scandens)*

age class** (x)	probability of surviving to age x (l_x)	average number of fledgling daughters (m_x)	product of survival and reproduction ($\Sigma l_x m_x$)
0	1.0	0.0	0.0
1	0.512	0.364	0.186
2	0.279	0.187	0.052
3	0.279	1.438	0.401
4	0.209	0.833	0.174
5	0.209	0.500	0.104

*The values are for the cohort of females born in 1975.

**Designated in years.

Source: Adapted from Peter R. Grant and B. Rosemary Grant, "Demography and the Genetically Effective Sizes of Two Populations of Darwin's Finches," Ecology, 73(3), 1992, copyright © 1992 The Ecological Society of America, used by permission.

Life table for one Darwin finch, the Galapagos cactus finch (Geospiza scandens)*

age class** (x)	probability of surviving to age x (l_x)	average number of fledgling daughters (m_x)	product of survival and reproduction ($\Sigma l_x m_x$)
6	0.209	0.833	0.174
7	0.209	0.250	0.052
8	0.209	3.333	0.696
9	0.139	0.125	0.017
10	0.070	0.0	0.0
11	0.070	0.0	0.0
12	0.070	3.500	0.245
13	0	—	—
			$R_0 = 2.101$

Net reproductive rate = $R_0 = \Sigma l_x m_x = 2.101$

Mean generation time = $T = (\Sigma x l_x m_x)/(R_0) = 6.08$ years

Intrinsic rate of natural increase of the population = r =

Life table for one Darwin finch, the Galapagos cactus finch (Geospiza scandens)*

age class** (x)	probability of surviving to age x (l_x)	average number of fledgling daughters (m_x)	product of survival and reproduction ($\Sigma l_x m_x$)
approximately 1nR_0 / T = 2.101/6.08 = 0.346			

The other value needed to calculate the rate at which the population can grow is the mean generation time (T). Generation time is the average interval between the birth of an individual and the birth of its offspring. To determine the mean generation time of a population, the age of the individuals (x) is multiplied by the proportion of females surviving to that age (l_x) and the average number of offspring left by females at that age (m_x). This calculation is performed for each age group, and the values are added together and divided by the net reproductive rate (R_0) to yield the result

$$T = \frac{\Sigma x l_x m_x}{R_o}$$

For example, the mean generation time of the Galapagos cactus finch is 6.08 years.

Another value is used by population biologists to calculate the rate of increase in populations that reproduce within discrete time intervals and possess generations that do not overlap. This is known as the intrinsic rate of natural increase (*r*), or the Malthusian parameter. Very simply, this rate can be understood as the number of births minus the number of deaths per generation time—in other words, the reproduction rate less the death rate. To derive this value using a life table, the natural logarithm of the net reproductive rate is divided by the mean generation time:

$$r = \frac{\ln R_O}{T}$$

Values above zero indicate that the population is increasing; the higher the value, the faster the growth rate. The intrinsic rate of natural increase can be used to compare growth rates of populations of a species that have different generation times. Some human populations have higher intrinsic rates of natural increase partially because individuals in those groups begin reproducing earlier than those in other groups. Mice have higher intrinsic rates of natural increase than elephants because they reproduce at a much earlier age and have a much shorter mean generation time.

If a population has an intrinsic rate of natural increase of zero, then it is said to have a stable age distribution and neither grows nor declines in numbers. A growing population has more individuals in the lower age classes than does a stable population, and a declining population has more individuals in the older age classes than does a stable population. Many human populations are currently undergoing population increase, far exceeding a stable age distribution. Although the global human population has increased almost continuously throughout history, it has skyrocketed since the Industrial Revolution, primarily because of a drop in death rates. No other species has shown such sustained growth.

Intrinsic rate of increase (r)* calculated for populations of species that differ greatly in their potential for the rate of population growth

species	intrinsic rate of increase (r)
elephant seal	0.091

*Values above zero indicate that the population is increasing. The higher the value of r, the faster the intrinsic growth rate of the population.

Source: Adapted from Robert E. Ricklefs, The Economy of Nature, 3rd edition, copyright © 1993 by W.H. Freeman & Company, used with permission.

Intrinsic rate of increase (r)* calculated for populations of species that differ greatly in their potential for the rate of population growth

species	intrinsic rate of increase (r)
ring-necked pheasant	1.02
field vole	3.18
flour beetle	23
water flea	69

Exponential and geometric population growth:

In an ideal environment, one that has no limiting factors, populations grow at a geometric rate or an exponential rate. Human populations, in which individuals live and reproduce for many years and in which reproduction is distributed throughout the year, grow exponentially. Exponential population growth can be determined by dividing the change in population size (ΔN) by the time interval (Δt) for a certain population size (N):

$$\frac{\Delta N}{\Delta t} = rN.$$

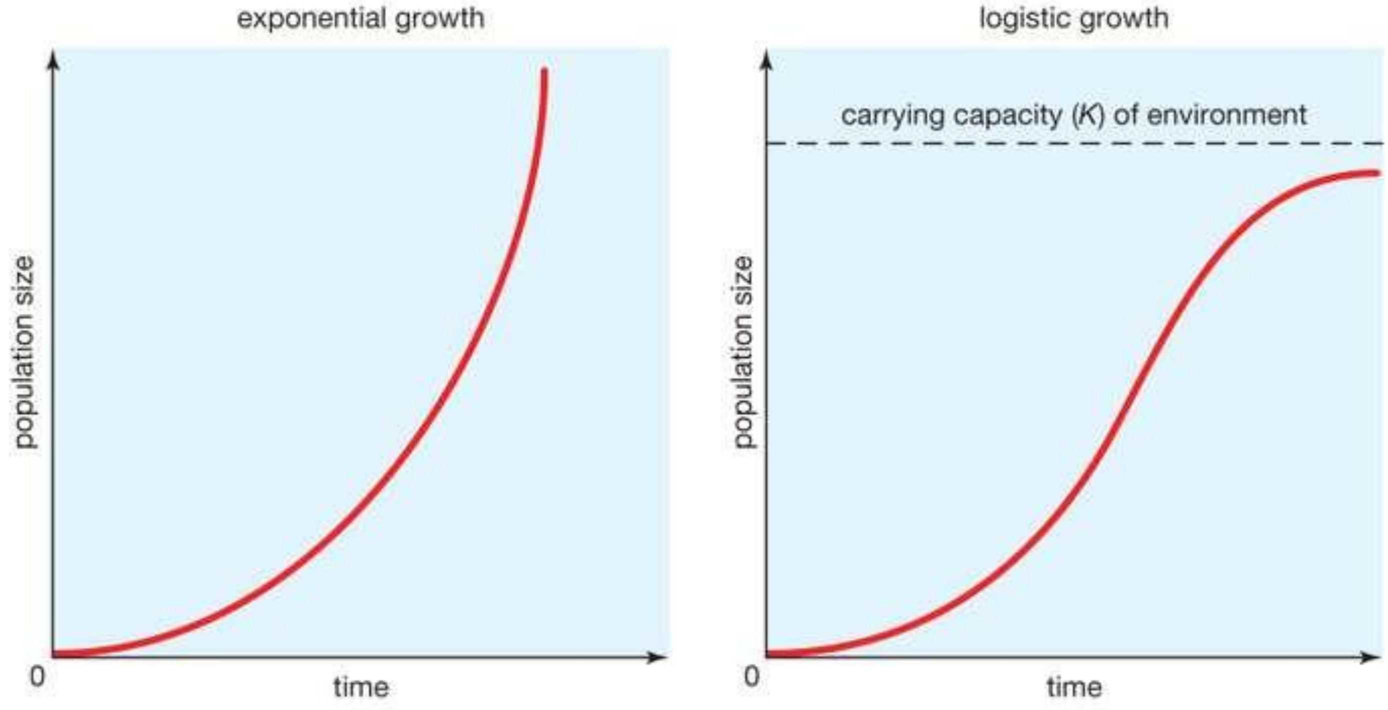
The growth curve of these populations is smooth and becomes increasingly steeper over time. The steepness of the curve depends on the intrinsic rate of natural increase for the population. Human population growth has been exponential since the beginning of the 20th century. Much concern exists about the impact this growth will have, not only on the environment but on humans as well. The World Bank projection for human population growth predicts that the human population will grow from 6.8 billion in 2010 to nearly 10 billion in 2050. That estimate could be offset by four population-control measures: (1) lower the rate of unwanted births, (2) lower the desired family size, (3) raise the average age at which women begin to bear children, and (4) reduce the number of births below the level that would replace current human populations (e.g., one child per woman).

Insects and plants that live for a single year and reproduce once before dying are examples of organisms whose growth is geometric. In these species a population grows as a series of increasingly steep steps rather than as a smooth curve.

Logistic population growth:

The geometric or exponential growth of all populations is eventually curtailed by food availability, competition for other resources, predation, disease, or some other ecological factor. If growth is limited by resources such as food, the exponential growth of the population begins to slow as competition for those resources increases. The growth of the population eventually slows nearly to zero as the population reaches the carrying capacity (K) for the environment. The result is an S-shaped curve of population growth known as the logistic curve. It is determined by the equation: $\frac{\Delta N}{\Delta t} = rN\left(\frac{K-N}{K}\right)$.

Exponential versus logistic population growth



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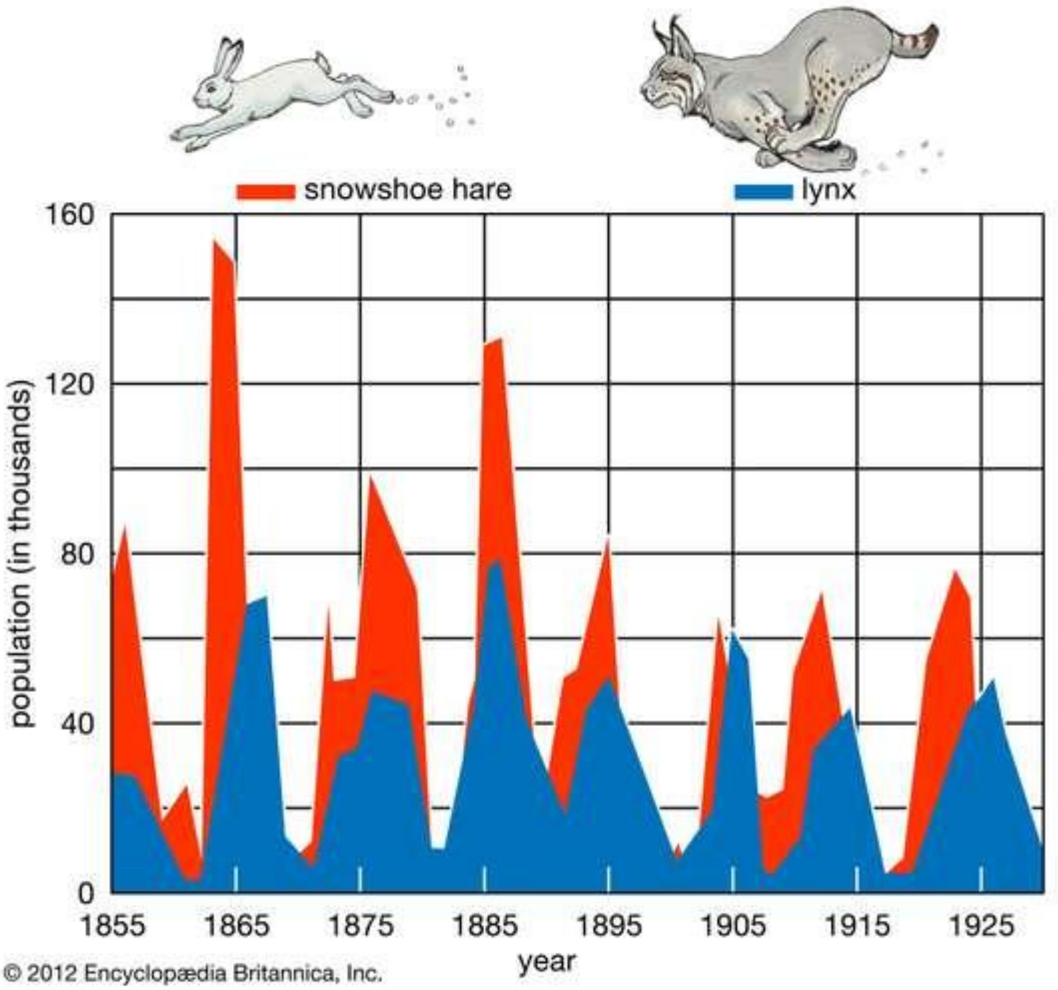
carrying capacity; exponential versus logistic population growth In an ideal environment (one that has no limiting factors) populations grow at an exponential rate. The growth curve of these populations is smooth and becomes increasingly steep over time (left). However, for all populations, exponential growth is curtailed by factors such as limitations in food, competition for other resources, or disease. As competition increases and resources become increasingly scarce, populations reach the carrying capacity (*K*) of their environment, causing their growth rate to slow nearly to zero. This produces an S-shaped curve of population growth known as the logistic curve (right).

Population fluctuation: As stated above, populations rarely grow smoothly up to the carrying capacity and then remain there. Instead, fluctuations in population numbers, abundance, or density from one time step to the next are the norm. Population cycles make up a special type of population fluctuation, and the growth curves in population cycles are marked by distinct amplitudes and periods that set them apart from other population fluctuations. In a few species, such as snowshoe hares (*Lepus americanus*), lemmings, Canadian lynx (*Lynx canadensis*), and Arctic foxes (*Alopex lagopus*), populations show regular cycles of increase and decrease spanning a number of years. The causes of these fluctuations are still under debate by population ecologists, and no single cause may provide an explanation for every species. Most major hypotheses link regular fluctuations in population size to factors that are dependent on the density of the population, such as the availability of food or the activities of specialized predators, whose numbers track the abundance of their prey through population highs and lows.



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Cyclical fluctuations in the population density of the snowshoe hare and its effect on the population of its predator, the lynx. The graph is based on data derived from the records of the Hudson's Bay Company.

Factors affecting population fluctuation: Population ecologists commonly divide the factors that affect the size of populations into density-dependent and density-independent factors. Density-independent factors, such as weather and climate, exert their influences on population size regardless of the population’s density. In contrast, the effects of density-dependent factors intensify as the population increases in size. For example, some diseases spread faster in populations where individuals live in close proximity with one another than in those whose individuals live farther apart. Similarly, competition for food and other resources rises with density and affects an increasing proportion of the population. The dynamics of most populations are influenced by both density-dependent and density-independent factors, and the relative effects of the factors vary among populations. Density-independent factors are known as limiting factors, while density-dependent factors are sometimes called regulating factors because of their potential for maintaining population density within a narrow range of values.

Population cycles: Because many factors influence population size, erratic variations in number are more common than regular cycles of fluctuation. Some populations undergo unpredictable and dramatic increases in numbers, sometimes temporarily increasing by 10 or 100 times over a few years, only to follow with a similarly rapid crash. For example, locusts in the arid parts of Africa multiply to such a level that their numbers can blacken the sky overhead; similar surges occurred in North America before the 20th century. The populations of some forest insects, such as the gypsy moths (*Lymantria dispar*) that were introduced to North America, rise extremely fast. As with species that fluctuate more regularly, the causes behind such sudden population increases are not fully known and are unlikely to have a single explanation that applies to all species.

The size of other populations varies within tighter limits. Some fluctuate close to their carrying capacity; others fluctuate below this level, held in check by various ecological factors, including predators and parasites. The tremendous expansion of many populations of weeds and pests that have been released into new environments in which their enemies are absent suggests that predators, grazers, and parasites all contribute to maintaining the small sizes of many population.

Fig:Invasive prickly pear cactus in Australia Area in Queensland, Australia, covered with prickly pear cactus (*Opuntia stricta*), an invasive species that rapidly expanded its range after being introduced there in 1926.*The Alan Fletcher Research Station, Department of Lands, Queensland*

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Fig:Biological control of invasive prickly pear cactus in Australia Area in Queensland, Australia, formerly covered with prickly pear cactus (*Opuntia stricta*). The cactus was introduced to the region in 1926, and three years later the moth borer (*Cactoblastis cactorum*) was introduced as a biological control agent to reduce populations of the cactus.*The Alan Fletcher Research Station, Department of Lands, Queensland*.

To control the explosive proliferation of these species, biological control programs have been instituted. With varying degrees of success, parasites or pathogens inimical to the foreign species have been introduced into the environment. The European rabbit (*Oryctolagus cuniculus*) was introduced into Australia in the 1800s, and its population grew unchecked, wreaking havoc on agricultural and pasture lands. The myxoma virus subsequently was released among the rabbit populations and greatly reduced them. Populations of the prickly pear cactus (*Opuntia*) in Australia and Africa grew unbounded until the moth borer (*Cactoblastis cactorum*) was introduced. However, many other similar attempts at biological control have failed, illustrating the difficulty in pinpointing the factors involved in population regulation.