**Population Ecology**

**Overview: Earth’s Fluctuating Populations**

* To understand human population growth, we must consider the general principles of population ecology.
* Population ecology is the study of populations in relation to the environment, including environmental influences on population density and distribution, age structure, and population size.

**Dynamic biological processes influence population density, dispersion, and demography**

* A population is a group of individuals of a single species that live in the same general area.
* Members of a population rely on the same resources, are influenced by similar environmental factors, and have a high likelihood of interacting with and breeding with one another.
* Populations can evolve through natural selection acting on heritable variations among individuals and changing the frequencies of various traits over time.

**Two important characteristics of any population are density and the spacing of individuals.**

* Every population has a specific size and specific geographical boundaries.
	+ The density of a population is measured as the number of individuals per unit area or volume.
	+ The dispersion of a population is the pattern of spacing among individuals within the geographic boundaries.
* Measuring density of populations is a difficult task.
	+ We can count individuals, but we usually estimate population numbers.
	+ It is almost always impractical to count all individuals in a population.
	+ Instead, ecologists use a variety of sampling techniques to estimate densities and total population sizes.
		- For example, they might count the number of individuals in a series of randomly located plots, calculate the average density in the samples, and extrapolate to estimate the population size in the entire area.
	+ Such estimates are accurate when there are many sample plots and a homogeneous habitat.
	+ A sampling technique that researchers commonly use to estimate wildlife populations is the mark-recapture method.
		- Individuals are trapped and captured, marked with a tag, recorded, and then released.
		- After a period of time has elapsed, traps are set again, and individuals are captured and identified.
		- The second capture yields both marked and unmarked individuals.
* From these data, researchers estimate the total number of individuals in the population.
* The mark-recapture method assumes that each marked individual has the same probability of being trapped as each unmarked individual.
* This may not be a safe assumption, as trapped individuals may be more or less likely to be trapped a second time.
	+ - Density results from dynamic interplay between processes that add individuals to a population and those that remove individuals from it.
	+ Additions to a population occur through birth (including all forms of reproduction) and immigration (the influx of new individuals from other areas).
	+ The factors that remove individuals from a population are death (mortality) and emigration (the movement of individuals out of a population).
	+ Immigration and emigration may represent biologically significant exchanges between populations.
* Within a population’s geographic range, local densities may vary substantially.
	+ Variations in local density are important population characteristics, providing insight into the environmental and social interactions of individuals within a population.
		- Some habitat patches are more suitable that others.
		- Social interactions between members of a population may maintain patterns of spacing.
* Dispersion is clumped when individuals aggregate in patches.
	+ Plants and fungi are often clumped where soil conditions favor germination and growth.
	+ Animals may clump in favorable microenvironments (such as isopods under a fallen log) or to facilitate mating interactions.
	+ Group living may increase the effectiveness of certain predators, such as a wolf pack.
* Dispersion is uniform when individuals are evenly spaced.
	+ For example, some plants secrete chemicals that inhibit the germination and growth of nearby competitors.
	+ Animals often exhibit uniform dispersion as a result of territoriality, the defense of a bounded space against encroachment by others.
* In random dispersion, the position of each individual is independent of the others, and spacing is unpredictable.
	+ Random dispersion occurs in the absence of strong attraction or repulsion among individuals in a population, or when key physical or chemical factors are relatively homogeneously distributed.
	+ For example, plants may grow where windblown seeds land.
	+ Random patterns are not common in nature.

**Demography is the study of factors that affect population density and dispersion patterns.**

* Demography is the study of the vital statistics of populations and how they change over time.
* Of particular interest are birth rates and how they vary among individuals (specifically females), and death rates.
* A life table is an age-specific summary of the survival pattern of a population.
* The best way to construct a life table is to follow the fate of a cohort, a group of individuals of the same age, from birth throughout their lifetimes until all are dead.
* To build a life table, we need to determine the number of individuals that die in each age group and calculate the proportion of the cohort surviving from one age to the next.
* A graphic way of representing the data in a life table is a survivorship curve.
	+ This is a plot of the numbers or proportion of individuals in a cohort of 1,000 individuals still alive at each age.
	+ There are several patterns of survivorship exhibited by natural populations.
	+ A Type I curve is relatively flat at the start, reflecting a low death rate in early and middle life, and drops steeply as death rates increase among older age groups.
		- Humans and many other large mammals exhibit Type I survivorship curves.
	+ The Type II curve is intermediate, with constant mortality over an organism’s life span.
		- Many species of rodent, various invertebrates, and some annual plants show Type II survivorship curves.
	+ A Type III curve drops slowly at the start, reflecting very high death rates early in life, then flattens out as death rates decline for the few individuals that survive to a critical age.
		- Type III survivorship curves are associated with organisms that produce large numbers of offspring but provide little or no parental care.
		- Examples are many fishes, long-lived plants, and marine invertebrates.
* Many species fall somewhere between these basic types of survivorship curves or show more complex curves.
	+ Some invertebrates, such as crabs, show a “stair-stepped” curve, with increased mortality during molts.
* Reproductive rates are key to population size in populations without immigration or emigration.
	+ Demographers who study sexually reproducing populations usually ignore males and focus on females because only females give birth to offspring.
	+ A reproductive table is an age-specific summary of the reproductive rates in a population.
		- The best way to construct a reproductive table is to measure the reproductive output of a cohort from birth until death.
		- For sexual species, the table tallies the number of female offspring produced by each age group.
		- Reproductive output for sexual species is the product of the proportion of females of a given age that are breeding and the number of female offspring of those breeding females.
	+ Reproductive tables vary greatly from species to species.
		- Squirrels have a litter of two to six young once a year for less than a decade, while mussels may release hundreds of thousands of eggs in a spawning cycle.

**Life history traits are products of natural selection**

* Natural selection favors traits that improve an organism’s chances of survival and reproductive success.
* In every species, there are trade-offs between survival and traits such as frequency of reproduction, number of offspring produced, and investment in parental care.
* The traits that affect an organism’s schedule of reproduction and survival make up its life history.

**Life histories are highly diverse, but they exhibit patterns in their variability.**

* Life histories entail three basic variables: when reproduction begins, how often the organism reproduces, and how many offspring are produced during each reproductive episode.
* Life history traits are evolutionary outcomes reflected in the development, physiology, and behavior of an organism.
* Some organisms, such as the agave plant, exhibit what is known as big-bang reproduction, in which an individual produces a large number of offspring and then dies.
	+ This is known as semelparity.
* By contrast, some organisms produce only a few offspring during repeated reproductive episodes.
	+ This is known as iteroparity.
* What factors contribute to the evolution of semelparity versus iteroparity?
* In other words, how much does an individual gain in reproductive success through one pattern versus the other?
	+ The critical factor is survival rate of the offspring.
	+ When the survival of offspring is low, as in highly variable or unpredictable environments, big-bang reproduction (semelparity) is favored.
	+ Repeated reproduction (iteroparity) is favored in dependable environments where competition for resources is intense.
		- In such environments, a few, well-provisioned offspring have a better chance of surviving to reproductive age.

**Limited resources mandate trade-offs between investment in reproduction and survival.**

* Organisms have finite resources, and limited resources mean trade-offs.
* Life histories represent an evolutionary resolution of several conflicting demands.
	+ Sometimes we see trade-offs between survival and reproduction when resources are limited.
	+ For example, red deer females have a higher mortality rate in winters following summers in which they reproduce.
* Selective pressures also influence the trade-off between number and size of offspring.
	+ Plants and animals whose young are subject to high mortality rates often produce large numbers of relatively small offspring.
		- Plants that colonize disturbed environments usually produce many small seeds, only a few of which reach suitable habitat.
		- Smaller seed size may increase the chance of seedling establishment by enabling seeds to be carried longer distances to a broader range of habitats.
	+ In other organisms, extra investment on the part of the parent greatly increases the offspring’s chances of survival.
		- Oak, walnut, and coconut trees all have large seeds with a large store of energy and nutrients to help the seedlings become established.
	+ In animals, parental care does not always end after incubation or gestation.
	+ Primates provide an extended period of parental care.

**The exponential model describes population growth in an idealized, unlimited environment**

* All populations have a tremendous capacity for growth.
* However, unlimited population increase does not occur indefinitely for any species, either in the laboratory or in nature.
* The study of population growth in an idealized, unlimited environment reveals the capacity of species for increase and the conditions in which that capacity may be expressed.
* Imagine a hypothetical population living in an ideal, unlimited environment.
* For simplicity’s sake, we will ignore immigration and emigration and define a change in population size during a fixed time interval based on the following verbal equation.

Change in population size = Births during - Deaths during during time interval

* Using mathematical notation, we can express this relationship more concisely:
	+ If N represents population size, and t represents time, then δN is the change is population size and ?t is the time interval.
	+ We can rewrite the verbal equation as:

δN/δt = B - D where B is the number of births and D is the number of deaths.

* We can convert this simple model into one in which births and deaths are expressed as the average number of births and deaths per individual during the specified time period.
* The per capita birth rate is the number of offspring produced per unit time by an average member of the population.
	+ If there are 34 births per year in a population of 1,000 individuals, the annual per capita birth rate is 34/1000, or 0.034.
* If we know the annual per capita birth rate (expressed as b), we can use the formula B = bN to calculate the expected number of births per year in a population of any size.
* Similarly, the per capita death rate (symbolized by m for mortality) allows us to calculate the expected number of deaths per unit time for a population of any size.
* Now we will revise the population growth equation, using per capita birth and death rates:

δN/δt = bN - mN

* Population ecologists are most interested in the differences between the per capita birth rate and the per capita death rate.
	+ This difference is the per capita rate of increase or r, which equals b ? m.
* The value of r indicates whether a population is growing (r > 0) or declining (r < 0).
* If r = 0, then there is zero population growth (ZPG).
	+ Births and deaths still occur, but they balance exactly.
* Using the per capita rate of increase, we rewrite the equation for change in population size as:

δN/δt = rN

* Ecologist use differential calculus to express population growth as growth rate at a particular instant in time:

dN/dt = rN

* Population growth under ideal conditions is called exponential population growth.
	+ Under these conditions, we may assume the maximum growth rate for the population (rmax), called the intrinsic rate of increase.
	+ The equation for exponential population growth is:

dN/dt = rmaxN

* The size of a population that is growing exponentially increases at a constant rate, resulting in a J-shaped growth curve when the population size is plotted over time.
	+ Although the intrinsic rate of increase is constant, the population accumulates more new individuals per unit of time when it is large.
	+ As a result, the curve gets steeper over time.
* A population with a high intrinsic rate of increase grows faster than one with a lower rate of increase.
* J-shaped curves are characteristic of populations that are introduced into a new or unfilled environment or whose numbers have been drastically reduced by a catastrophic event and are rebounding.

**The logistic growth model includes the concept of carrying capacity**

* Typically, resources are limited.
* As population density increases, each individual has access to an increasingly smaller share of available resources.
* Ultimately, there is a limit to the number of individuals that can occupy a habitat.
	+ Ecologists define carrying capacity (K) as the maximum stable population size that a particular environment can support.
	+ Carrying capacity is not fixed but varies over space and time with the abundance of limiting resources.
* Energy limitation often determines carrying capacity, although other factors, such as shelters, refuges from predators, soil nutrients, water, and suitable nesting sites can be limiting.
* If individuals cannot obtain sufficient resources to reproduce, the per capita birth rate b will decline.
* If they cannot find and consume enough energy to maintain themselves, the per capita death rate m may increase.
	+ A decrease in b or an increase in m results in a lower per capita rate of increase r.
* We can modify our mathematical model to incorporate changes in growth rate as the population size nears the carrying capacity.
* In the logistic population growth model, the per capita rate of increase declines as carrying capacity is reached.
* Mathematically, we start with the equation for exponential growth, adding an expression that reduces the rate of increase as N increases.
* If the maximum sustainable population size (carrying capacity) is K, then K ? N is the number of additional individuals the environment can accommodate and (K ? N)/K is the fraction of K that is still available for population growth.
* By multiplying the intrinsic rate of increase rmax by (K ? N)/K, we modify the growth rate of the population as N increases.
	+ dN/dt = rmaxN((K ? N)/K)
	+ When N is small compared to K, the term (K ? N)/K is large and the per capita rate of increase is close to the intrinsic rate of increase.
	+ When N is large and approaches K, resources are limiting.
		- In this case, the term (K ? N)/K is small and so is the rate of population growth.
* Population growth is greatest when the population is approximately half of the carrying capacity.
	+ At this population size, there are many reproducing individuals, and the per capita rate of increase remains relatively high.
* The logistic model of population growth produces a sigmoid (S-shaped) growth curve when N is plotted over time.
	+ New individuals are added to the population most rapidly at intermediate population sizes, when there is not only a breeding population of substantial size, but also lots of available space and other resources in the population.
	+ Population growth rate slows dramatically as N approaches K.
* How well does the logistic model fit the growth of real populations?
	+ The growth of laboratory populations of some organisms fits an S-shaped curve fairly well.
	+ These populations are grown in a constant environment without predators or competitors.
* Some of the assumptions built into the logistic model do not apply to all populations.
* The logistic model assumes that populations adjust instantaneously and approach the carrying capacity smoothly.
	+ In most natural populations, there is a lag time before the negative effects of increasing population are realized.
	+ Populations may overshoot their carrying capacity before settling down to a relatively stable density.
* Some populations fluctuate greatly, making it difficult to define the carrying capacity.
* The logistic model assumes that regardless of population density, an individual added to the population has the same negative effect on population growth rate.
	+ Some populations show an Allee effect, in which individuals may have a more difficult time surviving or reproducing if the population is too small.
	+ Animals may not be able to find mates in the breeding season at small population sizes.
	+ A plant may be protected in a clump of individuals but vulnerable to excessive wind if it stands alone.
* The logistic population growth model provides a basis from which we can consider how real populations grow and can construct more complex models.
	+ The model is useful in conservation biology for estimating how rapidly a particular population might increase in numbers after it has been reduced to a small size, or for estimating sustainable harvest rates for fish or wildlife populations.
* The logistic model predicts different per capita growth rates for populations of low or high density relative to carrying capacity of the environment.
	+ At high densities, each individual has few resources available, and the population grows slowly.
	+ At low densities, per capita resources are abundant, and the population can grow rapidly.
* Different life history features are favored under each condition.
	+ At high population density, selection favors adaptations that enable organisms to survive and reproduce with few resources.
		- Competitive ability and efficient use of resources should be favored in populations that are at or near their carrying capacity.
		- These are traits associated with iteroparity.
	+ At low population density, adaptations that promote rapid reproduction, such as the production of numerous, small offspring, should be favored.
		- These are traits associated with semelparity.
	+ Ecologists have attempted to connect these differences in favored traits at different population densities with the logistic model of population growth.
		- Selection for life history traits that are sensitive to population density is known as K-selection, or density-dependent selection.
			* K-selection tends to maximize population size and operates in populations living at a density near K.
		- Selection for life history traits that maximize reproductive success at low densities is known as r-selection, or density-independent selection.
			* r-selection tends to maximize r, the rate of increase, and occurs in environments in which population densities fluctuate well below K, or when individuals face little competition.
	+ Laboratory experiments suggest that different populations of the same species may show a different balance of K-selected and r-selected traits, depending on conditions.
	+ Many ecologists claim that the concepts of r- and K-selection oversimplify the variation seen in natural populations.

**Populations are regulated by a complex interaction of biotic and abiotic influences**

* Why do all populations eventually strop growing?
* What environmental factors stop a population from growing?
* Why do some populations show radical fluctuations in size over time, while others remain relatively stable?
* These questions have practical applications at the core of management programs for agricultural pests or endangered species.
* The first step to answering these questions is to examine the effects of increased population density on rates of birth, death, immigration, and emigration.
* Density-dependent factors have an increased effect on a population as population density increases.
	+ This is a type of negative feedback.
* Density-independent factors are unrelated to population density.

**Negative feedback prevents unlimited population growth.**

* A variety of factors can cause negative feedback on population growth.
* Resource limitation in crowded populations can reduce population growth by reducing reproductive output.
	+ Intraspecific competition for food can lead to declining birth rates.
* In animal populations, territoriality may limit density.
	+ In this case, territory space becomes the resource for which individuals compete.
	+ The presence of nonbreeding individuals in a population is an indication that territoriality is restricting population growth.
* Population density can also influence the health and thus the survival of organisms.
	+ As crowding increases, the transmission rate of a disease may increase.
	+ Tuberculosis, caused by bacteria that spread through the air when an infected person coughs or sneezes, affects a higher percentage of people living in high-density cities than in rural areas.
* Predation may be an important cause of density-dependent mortality for a prey species if a predator encounters and captures more food as the population density of the prey increases.
	+ As a prey population builds up, predators may feed preferentially on that species, consuming a higher percentage of individuals.
* The accumulation of toxic wastes can contribute to density-dependent regulation of population size.
	+ In wine, as yeast population increases, they accumulate alcohol during fermentation.
	+ However, yeast can only withstand an alcohol percentage of approximately 13% before they begin to die.
* For some animal species, intrinsic factors appear to regulate population size.
	+ White-footed mice individuals become more aggressive as population size increases, even when food and shelter are provided in abundance.
	+ Eventually the population ceases to grow.
	+ These behavioral changes may be due to hormonal changes, which delay sexual maturation and depress the immune system.
* All populations for which we have data show some fluctuation in numbers.
* The study of population dynamics focuses on the complex interactions between biotic and abiotic factors that cause variation in population size.
* Populations of large mammals, such as deer and moose, were once thought to remain relatively stable over time.
	+ A long-term population study of a moose population on Isle Royale has challenged that view.
	+ The population has had two major increases and collapses over the past 40 years.
* Large mammal populations do show much more stability than other populations.
	+ Dungeness crab populations fluctuated hugely over a 40-year period.
	+ One key factor causing these fluctuations is cannibalism.
		- Large numbers of juveniles are eaten by older juveniles and older crabs.
	+ In addition, successful settlement of crabs is dependent on water temperatures and ocean currents.
		- Small changes in these variables cause large fluctuations in crab population numbers.
* Immigration and emigration can also influence populations.
	+ This is particularly true when a group of populations is linked together to form a metapopulation.
* Some populations undergo regular boom-and-bust cycles, fluctuating in density with regularity.
	+ For example, voles and lemmings tend to have 3- to 4-year cycles.
	+ Ruffled grouse and ptarmigan have 9- to 11-year cycles.
* A striking example of population cycles is the 10-year cycles of lynx and snowshoe hare in northern Canada and Alaska.
* Three main hypotheses have been proposed to explain the lynx/hare cycles.
	+ The cycles may be caused by food shortage during winter.
	+ The cycles may be due to predator-prey interactions.
	+ The cycles may be affected by a combination of food resource limitation and excessive predation.
* If hare cycles are due to winter food shortage, they should stop if extra food is added to a field population.
* Researchers conducted such an experiment over 20 years.
* They found that hare populations increased, but that populations of lynx and hares continued to cycle.
* The first hypothesis can be discarded.
* Field ecologists have placed radio collars on hares, to find them as they die and determine the cause of death.
* 90% of dead hares were killed by predators; none appear to have died of starvation.
* These data support the second or third hypothesis.
* Ecologists tested these hypotheses by excluding predators from one area and by both excluding predators and adding food to another area.
* The results support the hypothesis that the hare cycle is driven largely by predation but that food availability also plays an important role, especially in winter.
* Perhaps better-fed hares are more likely to escape from predators.
* Many different predators contribute to these cycles, not only lynx.
* Long-term experimental studies continue to be conducted to help unravel the complex causes of these population cycles.

**Human population growth has slowed after centuries of exponential increase**

* The concepts of population dynamics can be applied to the specific case of the human population.
* It is unlikely that any other population of large animals has ever sustained so much population growth for so long.
* The human population increased relatively slowly until about 1650 when approximately 500 million people inhabited Earth.
* The Plague took a large number of lives.
* Since then, human population numbers have doubled three times.
* The global population now numbers more than 6 billion people, and is increasing by about 73 million each year, or 201,000 people each day.
* Population ecologists predict a population of 7.3–8.4 billion people on Earth by the year 2025.
* Although the global population is still growing, the rate of growth began to slow approximately 40 years ago.
	+ The rate of increase in the global population peaked at 2.19% in 1962.
	+ By 2003, it had declined to 1.16%.
* Current models project a decline in overall growth rate to just over 0.4% by 2050.
* Human population growth has departed from true exponential growth, which assumes a constant rate.
* The declines are the result of fundamental changes in population dynamics due to diseases and voluntary population control.
* To maintain population stability, a regional human population can exist in one of 2 configurations:

Zero population growth = High birth rates - High death rates.

Zero population growth = Low birth rates - Low death rates.

* The movement from the first toward the second state is called the demographic transition.
* After 1950, mortality rates declined rapidly in most developing countries.
	+ Birth rates have declined in a more variable manner.
* In the developed nations, populations are near equilibrium, with reproductive rates near the replacement level.
* In many developed nations, the reproductive rates are in fact below replacement level.
* These populations will eventually decline if there is no immigration and no change in birth rate.
* Most population growth is concentrated in developing countries, where 80% of the world’s people live.
* A unique feature of human population growth is the ability to control it with family planning and voluntary contraception.
	+ Reduced family size is the key to the demographic transition.
	+ Delayed marriage and reproduction help to decrease population growth rates and move a society toward zero population growth.
* However, there is disagreement among world leaders as to how much support should be provided for global family planning efforts.
* One important demographic variable is a country’s age structure.
* Age structure is shown as a pyramid showing the percentage of the population at each age.
	+ Age structure differs greatly from nation to nation.
	+ Age structure diagrams can predict a population’s growth trends and can point to future social conditions.
* Infant mortality, the number of infant deaths per 1,000 live births, and life expectancy at birth, the predicted average length of life at birth, also vary widely among different human populations.
	+ These differences reflect the quality of life faced by children at birth.

**Estimating Earth’s carrying capacity for humans is a complex problem.**

* Predictions of future human population vary from 7.3 to 10.3 billion people by the year 2050.
	+ Will Earth be overpopulated by this time?
	+ Is it already overpopulated?
	+ What is the carrying capacity of Earth for humans?
		- This question is difficult to answer.
		- Estimates of the answer have ranged from less than 1 billion to more than 1 trillion.
	+ Carrying capacity is difficult to estimate, and scientists have used different methods to obtain their answers.
		- Some use curves like those produced by the logistic equation to predict the future maximum human population size.
		- Others generalize from existing “maximum” population density and multiply by the area of habitable land.
		- Other estimates are based on a single limiting factor, usually food.
	+ Humans have multiple constraints. We need food, water, fuel, building materials, and other amenities.
	+ The concept of an ecological footprint summarizes the aggregate land and water area appropriated by each nation to produce all the resources it consumes and to absorb all the waste it generates.
	+ Six types of ecologically productive areas are distinguished in calculating the ecological footprint:
		- * Arable land (suitable for crops)
			* Pasture
			* Forest
			* Ocean
			* Built-up land
			* Fossil energy land (land required for vegetation to absorb the carbon dioxide absorbed by burning fossil fuels)
* Countries vary greatly in their individual footprint size and in their available ecological capacity (the actual resource base of each country).
* The overall analysis of human impact via ecological footprints suggests that the world is at or slightly above its carrying capacity.
* We can only speculate about Earth’s ultimate carrying capacity for humans, or about the factors that will eventually limit our growth.
	+ Perhaps food will be the main factor.
	+ Malnutrition and famine result mainly from unequal distribution, rather than inadequate production, of food.
	+ So far, technological improvements in agriculture have allowed food supplies to keep up with global population growth.
		- Environments can support a larger number of herbivores than carnivores.
	+ Perhaps we will eventually be limited by suitable space.
	+ Humans may run out of nonrenewable resources, such as certain metals or fossil fuels.
	+ The demands of many populations have already far exceeded the local and regional supplies of water.
		- More than one billion people lack access to sufficient water for basic sanitation.
	+ It is possible that the human population will eventually be limited by the capacity of the environment to absorb its wastes.
* Some optimists suggest that there is no practical limit to human population growth, due to our ability to develop technology.
* Exactly what the world’s carrying capacity is, and when and how we will approach it, are topics of great concern and debate.
* Unlike other organisms, we can decide whether zero population growth will be attained through social changes based on human choices or increased mortality due to resource limitation, war, or environmental degradation.