Chapter 48—Population Ecology

I. Populations
   A. Definition—a group of individuals from the same species that all live in the same area at the same time.
   B. Populations are the basic units of analysis in ecology and evolutionary biology.
   C. Ecology is the study of how populations interact with their environment.

II. Population Growth
   A. The fate of any population depends on four factors:
      1. Birthrate
      2. Death rate
      3. Immigration rate
      4. Emigration rate
   B. Births and immigration add individuals to the population, while deaths and emigration remove them.
   C. Basic Models of Population Growth
      1. When populations breed during discrete seasons, their growth can be calculated as \( \frac{N_1}{N_0} = \lambda \).
         a. \( N_0 \) is the population size at the beginning of the breeding season or starting point (time zero).
         b. \( N_1 \) is the population size one breeding interval later.
         c. \( \lambda \) is a parameter called the finite rate of increase
            (1) This is an observed rate of change over a given period of time.
            (2) It affects the shape of a function, but not its general nature.
      2. By rearranging the equation and stating it more generally, the size of a population at the end of time \( t \) can be expressed as \( N_t = N_0 \lambda^t \).
      3. A population’s per-capita rate of increase (rate of increase per individual) is symbolized by \( r \).
         a. The parameter \( r \) is defined as the per-capita birthrate minus the per-capita death rate.
         b. The parameter \( r \) is also called the instantaneous rate of increase.
      4. The relationship between \( \lambda \) and \( r \) is expressed as \( \lambda = e^r \), where \( e \) is the base of the natural logarithm, or about 2.72.
      5. By substitution, the equation \( N_t = N_0e^{rt} \) can be obtained.
         a. This equation summarizes how populations grow when they breed continuously, instead of at defined intervals or “breeding seasons.”
         b. This equation is often used to describe growth in human and bacterial populations.
      6. Graphs of discrete and continuous growth can be superimposed. (Fig. 48.2a)
      7. For seasonal breeders, \( r \) is the same as the growth rate expressed as the percent increase (or decrease) in the population per year.
   D. Exponential Growth
      1. Basic Concepts
         a. Exponential growth occurs when \( r \) does not change over time.
b. It does not depend on the number of individuals in the population.
c. Growth continues indefinitely because increases in the size of the population do not affect the overall growth rate.
d. An increased number of individuals are added as $N$ gets larger.
e. This type of growth is density independent. (Fig. 48.2b)

2. In reality, it is not possible for population growth to continue indefinitely.
   a. Individuals will always fill up all available breeding habitat and exhaust food supplies.
   b. If population density gets very high, the population’s per-capita birthrate decreases and the per-capita death rate increases. This will cause $r$ to decline.
   c. At high densities, growth should become density dependent.
   d. When density-dependent growth is graphed, it has three sections. (Fig. 48.3)

3. Carrying capacity is the maximum number of individuals that can be supported by the resources available in a habitat over a sustained period of time.
4. If the per-capita death rate of a population exceeds the per-capita birthrate, then $r$ becomes negative and the population declines.
5. Even though exponential growth can occur over short intervals, it cannot be sustained.

III. Case Studies Explaining How Population Size Changes over Time
   A. Density-Dependent Growth in Coral-Reef Fish
      1. Abundance of certain fish species varies from one coral reef to another.
      2. Two hypotheses exist regarding why:
         a. Density-dependent growth that is based on available resources in each reef
         b. Variation in immigration rates
      3. Tests of each hypothesis on the bridled goby. (Fig. 48.4a)
         a. Experiment
            (1) Created artificial reefs and stocked them with different densities of gobies, each of which was given an identifying mark.
            (2) After 2.5 months, analyzed the population on each reef to determine:
               (a) The growth rate of individuals
               (b) The survival rate of marked adults
               (c) The number of juveniles that successfully immigrated
         b. Results (Fig. 48.4b)
            (1) With increasing initial density, survival and recruitment decreased.
            (2) The final population of gobies on each artificial reef was remarkably similar, despite differences in initial density.
         c. Conclusions
            (1) The artificial reefs were so alike that their carrying capacity was nearly identical.
            (2) The results provide a clear example of density dependence in population growth.
         d. Could lack of food be responsible for limiting population growth on artificial reefs?
            (1) Found no relationship between initial population density and the growth rates of individual fishes.
Hypothesis—Higher rates of predation and/or disease, rather than food limitation, are likely the explanation for the results.

(a) Prediction—On natural reefs where goby population densities vary, marked differences should be found in predation rates or disease prevalence.

(b) This prediction has not yet been tested.

B. Are humans beginning to exhibit density-dependent growth?

1. The past and present size of the human population can be estimated using archeological, anthropological, and census-based data.

2. When graphed, the shape of the curve is remarkably similar to that of exponential growth. (Fig. 48.5a)

3. The human population has been increasing since 1400.
   a. The highest values occurred between 1965 and 1970.
   b. This was an increase of about 2.04% per year.

4. Since 1970, the growth rate has been dropping.
   a. The current rate of growth is 1.33% per year.
   b. The rate of growth in human populations is slowing for the first time in history.

5. To determine what the human population size will be at its peak, the UN Population Division bases its estimates on three different estimates of fertility.
   a. The current worldwide estimate of fertility is 2.7 children per woman.
   b. The UN estimates changes in population size based on average fertility rates of 2.5, 2.1, or 1.7. (Fig. 48.5b)
   c. The 2.1 value represents the replacement rate.
      (1) This is the average fertility rate required for each woman and man to produce exactly one offspring that survives long enough to breed.
      (2) At the replacement rate, \( r = 0 \).
   d. At a rate of 2.5, world population will be 10.7 billion in 2050 and show no signs of peaking.
   e. At a rate of 1.7, world population will be 7.3 billion in 2050 and will have already peaked.
   f. The UN had to alter its projections dramatically between 1992 and 1998 to account for the impact of AIDS.

6. Summary
   a. Humans are ending a period of rapid growth that has lasted well over 500 years.
   b. Changes in fertility and the AIDS epidemic will determine how fast the growth rates decline and how large the maximum population size eventually becomes.

C. Population Cycles

1. Some animal populations show regular fluctuations in their numbers.
   a. Example—Over 3/4 of the red grouse populations in Britain rise and fall in regular cycles (Figs. 48.6a and 48.6b). These cycles average 4 to 8 years.
   b. Most hypotheses to explain this phenomenon hinge on density dependence.

2. Investigations into why red grouse populations cycle.
   a. Hypotheses
      (1) The parasitic roundworm \( Trichostrongylus tenuis \) was responsible for the cycles.
      (2) Infection rates lessen when grouse densities are low, allowing populations to recover.
b. Experiment
(1) The researchers caught from 1000 to 3000 red grouse in each of several populations.
(2) Individuals caught were treated with a drug that kills roundworms and then released.
(3) They then monitored the number of birds shot by hunters in the ensuing years in each of the treatment populations.
(4) They compared their data to hunting success in two nearby populations where hunting intensity was comparable, but the birds were not treated with the drug.

c. Results (Fig. 48.6b)
(1) Control populations showed a typical dramatic four-year cycle in numbers.
(2) Treated populations maintained high densities.

d. Concluded: Red grouse cycles are driven by density-dependent changes in disease rates.

D. Recovering from Trauma
1. Natural and human-caused disasters can provide opportunities to study population growth in the context of recovery.
2. Example—the Exxon Valdez oil spill of 1989.
   a. 10 million gallons of oil were spilled into the Bligh Reef in Alaska’s Prince William Sound.
   b. This was the largest marine oil spill in U.S. history.
   c. Contact with oil had an immediate impact on seabird populations.
      (1) About 35,000 seabird carcasses were collected. (Fig. 48.7)
      (2) Current estimates place the death toll at 250,000.
   d. Most researchers hypothesized that most or all seabird populations would decline rapidly in oil-affected areas relative to pre-spill levels.
3. Stephen Murphy and colleagues set out to test this prediction.
   a. Experiment
      (1) They first estimated seabird population sizes and compared them to census numbers from counts taken in 1984–1985. This was done by counting the number of seabirds that were resting or flying within a 200-meter wide region extending from the high-tide transect line on shore out onto the water.
   b. Results
      (1) Seven of the 11 seabird species analyzed showed no significant response to oiling; their numbers did not change due to the oil spill.
      (2) One bird species actually showed a positive response to the oil spill. (Box 48.1)
      (3) Three species showed a negative response to the oil spill, but showed signs of recovery by the third year after the spill.
      (4) Other types of organisms were very negatively affected by the oil spill.
   c. Conclusions
      (1) Enough individuals may have immigrated from nearby populations to make up for the losses in oiled areas.
      (2) The availability of immigrants from nearby populations affected the recovery of many species.
(3) Recovery has been very slow for species that depend on habitats where oil has persisted. *(Figs. 48.8a and 48.8b)*

(4) Populations are generally able to recover from catastrophic losses if the habitat is allowed to recover.

(5) The recovery process is rapid if nearby populations serve as a source of immigration.

IV. Population Structure

A. In any population study, it is critical to know how many reproductively active individuals there are versus juveniles that are too young to reproduce.

B. Age Structure

1. Developed nations have an age distribution that tends to be even.
   a. Such nations have similar numbers of people in most age classes. *(Fig. 48.9a)*
   b. This results from long periods of no or very slow population growth.
   c. Populations of developed nations are not expected to grow very quickly.

2. Developing nations have an age distribution that is bottom-heavy.
   a. Such nations are dominated by very young individuals. *(Fig. 48.9b)*
   b. This results when populations have undergone a period of rapid growth.
   c. Extremely rapid growth can be expected to continue in these nations.

C. Geographic Structure

1. The habitat preferences of many species are restricted.
   a. Individuals occupy only isolated patches within a broad area.
   b. Many species exist as a metapopulation; that is, a population made up of many small populations that are isolated in fragments of habitat. *(Fig. 48.10)*

2. Over time, each population within a larger metapopulation is likely to go extinct

3. Immigration from nearby habitats can reestablish populations in empty fragments of habitat, thereby maintaining a stable number of individuals.

4. The metapopulation concept began as a purely theoretical idea, but have been confirmed on studies of the Glanville fritillary butterfly. *(Fig. 48.11)*

1. Experiment
   (a) Research began with a survey of meadow habitats on the islands.
   (b) Because the butterfly feeds on just two host plants, they were able to pinpoint potential butterfly habitats.
   (c) Population size in each patch of habitat was estimated by counting the number of larval webs in each.
   (d) To determine whether migration among these patches occurs, they conducted a mark-recapture study. *(Box 48.2)*

2. Results
   (a) Of the 1,502 meadows that contained host plants, 536 contained Glanville fritillaries.
   (b) Most of these had only a single larval group, with the largest population containing 3,450 larvae.
   (c) Of the 1,731 butterflies that they marked and released, 741 were recaptured over the course of the summer.
   (d) Of the recaptured individuals, 9% were found in a new habitat patch.
(e) After repeating the experiment two years later, the researchers confirmed results that some populations had gone extinct and others had been created.

(3) Conclusions
(a) Migration rates were high enough to suggest that patches where a population has gone extinct will eventually be recolonized.
(b) The metapopulation model is valid, and metapopulations do exist in nature.
(c) Small, isolated populations, even those on nature reserves, are unlikely to survive over the long term.
   i. Conservation biologists are designing reserves for threatened species that are sizable enough to maintain large populations.
   ii. Systems of small reserves, all connected by corridors of habitat, can be constructed as an alternative.
   iii. It is also crucial to preserve some patches of currently unoccupied habitat.

V. Demography and Conservation
   A. Demography is the study of factors that determine the size and structure of populations through time.
      1. Biologists need to know other factors besides age and geographic structure.
         a. How likely it is that individuals in each age group will survive to the following year.
         b. How many offspring are produce by females of different ages.
         c. How many individuals of different ages immigrate and emigrate each generation.
      2. Demographic data provide an important tool for biologists.
   B. Life Tables
      1. Formal demographic analyses of populations are based on a type of data set called a life table.
         a. Life tables were invented in Rome almost 2000 years ago.
         b. Biologists and insurance agencies use them in modern times.
         c. A life table summarizes the probability that an individual will survive and reproduce in any given year over the course of its lifetime.
      2. Example—data collected on the lizard *Lacerta vivipara*. (Fig. 48.12)
         a. Goal was to estimate a life table for a low-elevation population and then compare the results to that of other populations.
         b. Their work was “pure”; that is, it was not motivated to solve an applied problem.
      3. Life tables contain many pieces of information. (Table 48.1)
         a. Survivorship—proportion of offspring produced that survive, on average, to a particular age.
            (1) Symbolized by $l_x$.
            (2) Can be calculated as $l_x = N_x / N_0$.
         b. When the number of survivors is plotted versus age, a survivorship curve results.
            (1) There are three general types of survivorship curves—type I, II, and III. (Fig. 48.13)
            (2) Humans have type I, songbirds type II, and many plants type III.
c. Fecundity—number of female offspring produced by each female in the population.
   (1) In general, biologists keep track of only females when constructing a life table.
   (2) Symbolized by \( m_x \).

d. The net reproductive rate, \( R_0 \), can be calculated as: \( R_0 = \sum l_x m_x. \)
   (1) If it is greater than 1, the population is increasing in size.
   (2) If it is less than 1, the population is declining.

4. Life-table data can be used to make population projections.
   a. The data can help solve applied problems related to saving endangered species. (Fig. 48.14a, b, and c)
   b. The data can be used to predict many aspects of the future of populations.
   c. Population projections made from life-table data may be too simple to be useful.

5. Life-table data can be used to guide conservation programs.
   a. Values for survivorship and fecundity at particular ages can be altered, and the consequences of doing so can be analyzed.
   b. Analysis allows biologists to determine which aspects of survivorship and fecundity are sensitive to particular species.
      (1) Endangered species tend to have high juvenile mortality, low adult mortality, and low fecundity.
      (2) In humans and other species with high survivorship across almost all age classes, rates of population growth are extremely sensitive to changes in age-specific fecundity.
   c. Conservationists may need to expand the basic demographic models to account for occasional disturbances and other disasters.

C. Population Viability Analysis (PVA)
   1. PVA is a model estimating the likelihood that a population will avoid extinction for a given time.
   2. PVAs combine basic demographic models with data on geographic structure and the rate and severity of habitat disturbance.
   3. Populations are considered viable if the analysis predicts that it has a 95% probability of surviving for at least 100 years.
   4. Natural resource managers are currently using PVA.
      a. The effects of logging, development, and other land management practices are assessed.
      b. The merits of alternative recovery plans for endangered species can be evaluated.
      c. Example—a study of Leadbeater’s possum, an endangered marsupial, (Fig. 48.15a and b)
         (1) Experiment
            (a) The researchers used previously obtained life-table data for this rare and reclusive species, even though it was difficult to collect.
            (b) Enough life-table data existed to conduct an analysis and make population projections.
         (2) Results
            (a) When migration is high, the overall population size is predicted to stabilize at about 70 individuals.
(b) When no migration occurs, the final population size is predicted to be less than 20 individuals.

(3) Their main conclusion was that extensive timber harvesting would pose a serious threat to this species.

5. PVA makes many assumptions about future events, and is only as accurate as the data entered into it.

6. The usefulness of PVA has been challenged because basic demographic information is lacking or poorly documented in many endangered species.

7. But recent research has found that the predictions of many PVAs have correlated very closely with what actually occurred in nature.