LECTURE 12
Regulation of Population Growth

I. Regulation of population growth.
   1. As Darwin recognized, exponential growth cannot go on very long - resource limitation.
   2. If B decreases and D increases, then \( r \) decreases.

A. Logistic model.
   1. If resources are finite, then there is some maximum population size that the habitat can support.
      a. Call that number the **carrying capacity**, symbolized \( K \). This is the maximum density of population that the environment can support over a sustained period. \( K \) is unique for each species.
   2. Thus, a model of population regulation should have following properties
      a. If \( N < K \), rate of growth should slow as \( N \to K \).
      b. If \( N > K \), rate of growth should be negative.
      c. For \( N=K \), \( \Delta N=0 \)
      d. This is a simplified model of how rate of population growth should change as \( N \) changes relative to \( K \).
   3. Changing growth produce a sigmoid shape curve.
      a. During the acceleration stage, births exceed deaths. \( N \) is well below \( K \) and \( r \) is positive.
      b. As \( N \) approaches \( K \), the birth rate declines or the death rate increases, and \( r \) decreases.
      c. If \( N=K \), then rate of growth should be zero; \( \Delta N=0 \). \( r=0 \).
      d. If \( N > K \), rate of growth should be negative. \( (r \) is negative).
   4. Mathematical model is modified so that the value of \( r \) is reduced as \( N \) increases
      a. The maximum sustainable population is \( K \).
      b. \( (K-N) \) indicates how many additional individuals can be added to the environment.
      c. \( K-N/K \) is the proportion of \( K \) (the total) that can be added.
      d. Resulting growth equation. \( dN/dt = rN (K-N/K) \)
         can be written as \( \frac{dn}{dt} = rN \left(1 - \frac{N}{K}\right) \).
   5. Population growth is no longer a function of the intrinsic rate of growth, \( r \), and the population size, \( N \), but also by the relationship of \( N \) with the carrying capacity.
   6. Equilibrium species also called "**K-selected**" - These are species that live at a density near the limit of imposed resources.

B. Does this model actually predict real population growth? Examples: (See Campbell, Chap. 47).
   1. *Paramecium aurelia* - The growth of many small organisms, if kept under optimal conditions, will exhibit a classical sigmoid growth curve.
   2. Daphnia ("water flea", small crustacean) overshoot the carrying capacity of the population. This is known as a **lag** effect.
   3. Assumptions of model not always met. E.g. the **Allee effect** - there is some minimum population below which the population will decline (instead of increase).
   4. Logistic growth entails many important assumptions. Five of the most important include:
      i. The relation between density and rate of increase is linear.
      ii. The effect of density on rate of increase is instantaneous.
      iii. The environment (and thus \( K \)) is constant.
      iv. All individuals reproduce equally.
      v. There is no immigration or emigration.
   5. Assumptions are easily met for laboratory cultures, but not for field populations of larger animals.
      a. Fur seals oscillating around \( K \)
b. Sheep in Australia. Oscillations, not logistic, but cyclical. N is close to K, so r is small but not near $r_{max}$.

c. Even worse, reindeer introduced onto two islands in 1911.

6. In the case of field populations, assumptions of logistic model are not so easily met.
   i. In nature, each individual added to the population probably does not cause an incremental decrease to r.
   ii. In nature there are often time lags, especially in species with complex life cycles. For example, in mammals it may be months before pregnant females give birth even when resources have been favorable for months.
   iii. In nature, K may vary seasonally or with climate.
   iv. In nature, often a few individuals command many matings.
   v. In nature there are few barriers preventing dispersal.

7. Important point: logistic, like all models, is not universal. Simply one model that works well for some cases, but not for others.

II. Density dependent regulation vs. density independent regulation (non-equilibrium approach)

A. Density-dependent factor is one that intensifies as population increases in size. In large populations, density-dependent factors affect more individuals and have larger effect on each. Result: decreased birth and increased death rates.

1. Density dependent factors result from either intraspecific or interspecific competition

2. Only density dependent factors can produce logistic type growth. Why? Because logistic growth is dependent upon a carrying capacity, i.e. N in an environment.
   a. However, density dependent factors not the only factors regulating population size.

B. Density independent factors – the occurrence and magnitude of effect is uncorrelated with population size. Most result from climate and weather.

1. Example: drought will reduce N, but obvious that occurrence of drought is not related to population size.

2. Can be important in population regulation because, if density-independent factors occur often enough, may prevent N ever approaching K. (in fact, there is no K, or equilibrium)

3. Concept of non-equilibrium brought to light by Andrewartha and Birch (entomologists).

4. Example: Thrips, small insects, ubiquitous, live in Australia, eat pollen and flowers of rose family. See Campbell, Chapter 47.
   a. Number of Thrips determined by number of flowers, which is determined by weather, seasons.
   b. In the winter, cool temperatures slow down the development of the thrips so that do not complete development before the flower dies and falls to the ground. N is small during winter (some flowers remain year-round, but numbers are low).
   c. In the Spring (December), the thrip population grows when flowers bloom. The heat of the summer reduces the population density before it can density-dependent factors come into play.
   d. Result: Exponential growth, then crash. Not like reindeer (thrips don't overgraze).

5. In reality, both density independent and density dependent factors probably operate on most populations.

E.g., Thrips crash during mid-summer is density-independent- related to climate. But starting population in Spring is probably due to density-dependent regulation- the number of available flowers. The number of flowers is determined by winter weather (may be considered density independent), but the starting population each year may be determined by a limiting resource- number of flowers. (That’s my take on it.)