

Lecture 14: Population growth.

Outline

Exponential growth

- Discrete breeding seasons, nonoverlapping generations, semelparous life history
 - Discrete breeding seasons, overlapping generations, iteroparous life history
 - Continuous breeding seasons, overlapping generations, iteroparous life history
- General properties of exponential growth models
Consequences of exponential growth

Density-independent and density-dependent limiting factors

Density dependent population growth: logistic equation

- Continuous breeding seasons, linear density dependence (Verhulst-Pearl eqn)
- Discrete breeding seasons, linear density dependence
- Discrete breeding seasons, nonlinear density dependence
 - Compensation, overcompensation, undercompensation

Limitations, assumptions, usefulness of these models

Introduction

The goal of the next two lectures is to understand the processes that cause changes in population size through time. A second goal is to understand simple mathematical models that describe population growth. We'll start with the simplest models for single species, and add to them to become progressively more realistic (adding effects of intraspecific competition, interspecific competition & predation). A *lot* of the theory underlying ecology and population biology is based on extensions of these models, so it is critical to understand them well.

Exponential population growth

(Pianka Fig. 9.1)

The simplest type of population growth is exponential, as shown by reindeer on Pribilof Islands for 30 years after introduction. Exponential growth occurs when a single species is not limited by other species (no predation, parasitism, competitors), resources are not limited, and the environment is constant. These conditions called an 'ecological vacuum', and this does not often occur (for long) in nature. But colonizations like the reindeer example, or recovery of a population after a large-scale disturbance (fires, crash from disease) can allow exponential growth for a period.

How do we build a model of exponential population growth?

1. Consider an animal like *Antechinus*, Australian marsupial mouse. *Antechinus* are seasonal breeders that mature at age 1 year. Males mature, fight like mad, mate like mad, and all die (due to a huge pulse of the stress hormone corticosterone). Females live a few weeks longer, but just long enough to raise a litter, then die after weaning.

This life history shows:

- ***discrete breeding seasons***
- ***nonoverlapping generations***
- ***semelparous life history***

How do you know if an *Antechinus* population is growing or not? From demography lectures, $R_0 = \sum l_x m_x$. R_0 is the ***average number of offspring produced by an individual in its lifetime***, called the ***net reproductive rate***, or the ***net replacement rate***. As long as survivorship (l_x) and fecundity (m_x) stay the same, R_0 can be used to project the number of mice in the population one generation from now:

N_0 = number in population now

N_1 = number in population one generation later

$$N_1 = N_0 R_0$$

In turn, the population of N_1 will grow by the same rule (initial population size * R_0) over the next generation:

$$N_2 = N_1 R_0$$

Substituting for N_1 gives:

$$N_2 = N_0 R_0^2$$

Generalizing:

$$N_t = N_0 R_0^t$$

Which gives the population size t generations in the future. This is the most basic ***discrete population growth model***, from which all others are derived. It models exponential growth because it assumes that R_0 is constant \Rightarrow it assumes that survival and fecundity do not decrease as the population gets larger.

2. The marsupial mouse has unusual life-history for a mammal (though it's common among invertebrates). A more typical mammalian life history is shown by African wild dogs, which breed one a year (in the dry season, when prey is more easily caught), but individuals breed repeatedly in a lifetime, and have overlapping generations.

This life history shows:

- *discrete breeding seasons*
- *overlapping generations*
- *iteroparous life history*

Modify the population growth model, by projecting population size t *breeding seasons* in the future, rather than t *generations* in the future:

$$N_t = N_0 \lambda^t$$

The only change from previous model is that change in population size is measured in units of time (years, for wild dogs) rather than units of generations. R_0 , a measure of change per generation, is replaced by R , a measure of change per time.

R is called the *fundamental net reproductive rate*. To calculate λ from life table data:

$\ln \lambda = \ln R_0 / T$ where T is length of a generation, described in an earlier lecture.

3. Another common life-history for mammals is similar to the wild dogs' but individuals breed continuously, rather than in discrete breeding seasons. For example, white footed mice in much of the midwest breed continuously through the spring and summer, so that a mother continues to breed without a pause even after her daughters have matured and are breeding.

This life history shows:

- *continuous breeding*
- *overlapping generations*
- *iteroparous life history*

Continuous population growth models are easiest to understand by starting with the *rate of population change*, rather than population size itself.

$$\begin{aligned} dN/dt &= \text{change in \# of animals/change in time} \\ &= (N_t - N_0)/(t-0) \\ &= \text{'recruitment rate'} \end{aligned}$$

The recruitment rate of an exponentially growing population is influenced by two things:

- i. r the per-capita rate of increase

$$r = (b + i) - (d + e).$$

Where b = per-capita birth rate/time, d = per-capita death rate/time, i = immigrants per individual/time, e = emigrants/individual/time. If population is closed:

$$r = b - d.$$

Relationship of r to R_0 is:

$$r = \ln R_0 / T$$

Also, $r = \ln(\lambda)$ and $\lambda = e^r$

The units of r are individuals gained or lost/individual/time, which reduces to simply 1/time.

ii. N In addition to the per-capita growth rate (r), the recruitment rate dN/dt is also affected by the number of individuals already present to reproduce and die (N); population of 10 individuals growing at $r = 0.1$ individuals gained/individual/year will increase by 1 individual/year, but 100 individuals growing at $r = 0.1$ will increase by 10 individuals/year

$$dN/dt = rN$$

Integrate both sides of this equation,

$$N_t = N_0 e^{rt} \quad (e \text{ is the base of natural logarithm, } 2.71818)$$

Properties of exponential population growth models.

The discrete and continuous population growth models described above are similar in four important ways:

- 1) R and r are both ***net*** measures of an individual's contribution to population growth. Both are influenced by births (b, m_x) and by deaths (d, l_x).
- 2) R and r are both ***per-capita*** measures, of individual contribution to population growth. (dN/dt , recruitment, is a population measure).
- 3) R and r are ***constants***, in these simple models. In these simple models of exponential growth, birth and death rates stay the same through time, regardless of population size. They are ***density-independent***. This will be modified as we deal with intraspecific competition, which creates density-dependent population growth.

Consequences of exponential population growth.

How long does an exponentially growing population take to double? This is equivalent to asking how long t is, when $N_t = 2N_0$.

Using exponential growth equation,

$$N_t = N_0 e^{rt}, \text{ substitute } 2N_0 \text{ for } N_t,$$

$$2N_0 = N_0 e^{rt}$$

$$\ln 2 = rt$$

$$t = \ln 2 / r$$

$$\text{doubling time} = 0.7/r$$

This equation for doubling time works for any process of exponential growth. Some everyday examples:

3.5% inflation means that prices will double (value of dollar will halve) in $0.7/0.035 = 20$ years.

Typical credit card debt has annual interest (APR) of 18%. The amount you owe doubles in $0.7/0.18 \approx 4$ years (!)

Human energy use has been increasing at 5% per year. In the next $0.7/0.05 = 14$ years, energy use will double.

Global CO₂ emissions are increasing exponentially at about 1% per year, so the atmospheric CO₂ concentration will double in about $0.7/0.01 = 70$ years.

2. Point 1 makes it clear that exponential quickly growth accelerates to become extremely rapid. Because of this, ***exponential growth is always temporary***, and depends on the existence of an 'ecological vacuum'. As a population grows, it will eventually be limited by one or more ecological factors (e.g. shortage of food).

Density-dependent and density-independent limits on population growth

What stops exponential growth, or prevents it from beginning at all? Remember that exponential growth models assume that *birth and death rates are constant* (r or R constant). In the real world, birth and death rates *change over time*, and these changes can limit population growth.

Two general classes of limiting factors:

Density-independent limiting factors: reduce population growth regardless of population size.

(Pianka Fig. 9.1) Example with reindeer on Pribilofs.

Can use this plot to back-calculate $R = N_{t+1}/N_t$.

Year	Pop. Size	R
1910	20	1.2
1915	80	1.4 (density increases, R increases)
1920	180	1.4 (density increases, R stays same)
1925	180	1.2 (density stays same, R decreases)
1930	350	1.2
1935	1100	1.3

Also, in 1921-1922, R is negative at densities (pop size) that gave positive R in other years. Overall, R varies from year to year, but changes are not related to population density.

(Note for later: = in computer simulations of density dependent growth with time lags, you'll see very similar patterns to this one, so telling density dependent and density independent changes apart can be difficult in particular cases).

Density-independent limiting factors:

1. Are usually physical in nature (hard winters, failure of rainy season).
2. Are more important for small organisms, because small organisms are not as well buffered against physical environment.
3. Are more important in extreme or highly seasonal environments than in mild, stable environments.
4. Can interrupt exponential growth or cause declines, but **cannot regulate a population at a stable population size.**

Density-dependent limiting factors: reduce population growth with an impact that depends on current population size.

Examples:

(Fig 2-11 Gotelli) *survival and reproduction decrease as population size increases in Song Sparrows on Mandarte Island*

(Tables 17-2 and 17-3 Ricklefs) *reproduction in w-t deer declines as population density increases*

(Fig 17-7 Ricklefs) experimental example: *mortality increases as density increases* in grain beetles.

For all of these examples, the density-dependent limiting factor is probably intraspecific competition for limited food.

Density-dependent limiting factors:

1. Are usually biological in nature (competition, disease, predation).
2. Are more important for large organisms (which are buffered from physical environment).
3. Are more important in physically benign and constant environments.
4. Can interrupt exponential growth or cause declines, and ***CAN regulate a population near a stable population size.***

Density-dependent population growth.

A (closed) population is growing when births exceed deaths: $r = b - d > 0$.

If birth or death rates are affected by density dependent factors, plotting b and d against population size predicts where per-capita birth and death rates will exactly balance and population size will stabilize ($dN/dt = 0$). The stable point is called the ***carrying capacity, K.***

(Fig. 6.9 Begon et al.) Per-capita birth and death rates b & d vs N .

Viewing this in terms of number of individuals, rather than per-capita rates, see that density dependent growth follows an S-shaped “logistic”, “sigmoid” curve.

(Fig 6.10 Begon et al)

Logistic growth curves are common in nature: grain beetles, wildebeest, willows

(Fig. 6.13 Begon et al.) note that the grain beetles were used to show density dependent death rates above.

Logistic population growth models

How do we modify exponential growth models to take account of density-dependent limits on growth?

1. This is easiest to show for *continuous breeding seasons*.

The exponential growth model for continuous breeding is:

$$dN/dt = rN$$

Simplest way to incorporate density dependence is to assume that b declines and/or d increases in straight line fashion as N increases.

(Fig. 9.5 Pianka)

In this case (linear density dependence),

(Fig. 9.2 Pianka)

actual per-capita rate of increase $\approx r$ when $N = 1$

actual per-capita rate of increase = 0 when $N = K$

$$dN/dt = rN[(K - N)/K]$$

Linear decline in the actual per-capita rate of increase is incorporated via a new term,

$(K - N)/K$, which is the *proportion of the habitat's carrying capacity that is not being used*.

When N is near 0, $(K-N)/K$ is near 1 and growth (dN/dt) is nearly exponential (rN).

When N is near K , $(K-N)/K$ is near 0 and growth (dN/dt) nearly stops.

2. For *discrete breeding seasons*, the equation for linear density dependent population growth is slightly different, but has the same property of slowing growth as population size increases.

$$N_{t+1} = \frac{N_t R}{1 + aN_t}$$

Logic of this equation similar to Verhulst-Pearl equation. This equation also models linear density dependence, with population growth, R , slowed by a factor $(1+aN_t)$, as N increases.

For a population with weak density dependence, $a \approx 0$, $(1+aN_t) \approx 1$, growth nearly exponential (RN_t)

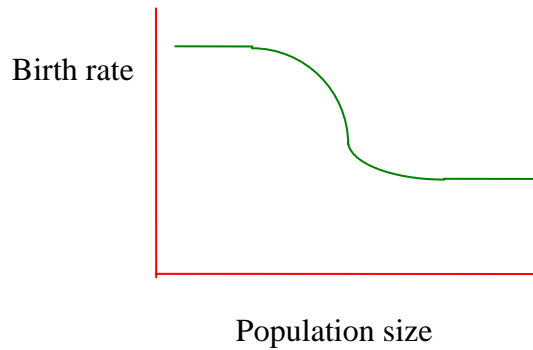
For a population with strong density-dependent effects on growth, a is large. As N_t increases, aN_t increases, and slows the growth rate.

3. The equation for density dependent growth with discrete breeding seasons can be modified to deal with *non-linear density dependence*.

Up to now, we've assumed that birth rates decline or death rates increase in a linear manner as population size increases

(Fig. 9.5 Pianka)

Often, the density-dependence won't actually be linear. E.g.



This kind of non-linear density dependent population growth can be modeled with a minor revision to the equation:

$$N_{t+1} = \frac{N_t R}{1 + (aN_t)^b}$$

$b = 1$, then density dependence is linear: ‘compensating’ density dependence

$b < 1$, ‘undercompensating’ density dependence

$b > 1$, ‘overcompensating’ density dependence

(Fig 6.4 Begon et al)

Compensating density dependence \Rightarrow increase in death rate and/or decrease in birth rate exactly offsets any change in population size, so that the population stays at the same size.

Undercompensating \Rightarrow death rate increases and/or birth rate decreases as population size goes up, but the change is not great enough to keep population from continuing to grow.

Overcompensating \Rightarrow death rate increases and/or birth rate decreases as population size goes up, so strongly that an initial increase in population size will result in a population decline. (E.g. overeating resources)

(Fig 6.3 Begon et al)

(Fig 6.5 Begon et al)

(Fig 6.6 Begon et al)

Assumptions of these models

1. Constant carrying capacity.
2. All individuals are identical (intraspecific competition has same effect on everyone).
3. Linear density dependence (in the Verhulst Pearl equation for continuous breeding seasons; modified this in discrete equation).
4. No impact of other species on population growth (can modify this).
5. No time lag in effect of density on population growth (can modify this).