

Today's Objectives

- Review **factors** that influence population growth
- Distinguish between **density independent** and **density dependent** factors
- Understand the mechanism and assumptions of the following control functions for population growth:
 - logistic equation
 - modified logistic
 - logistic with refuge
 - Monod
- Plot control functions to evaluate their operation

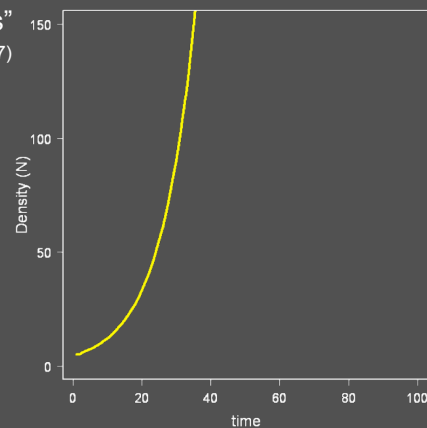
Review: Exponential Growth

"First principles of population dynamics"

(Berryman 1997)

$$\frac{dN}{dt} = rN$$

Population density
Intrinsic growth rate
 $r = b - d$



Assumes ...

1. Identical individuals (genetic, age, size)
2. Closed population
3. Continuous time, no lags
4. Constant $r = b - d$
5. No limits to growth

Problem: Natural populations don't grow without bounds.

Borrett 2008

What factors influence population growth?

As more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either **one individual with another of the same species**, or with **individuals of distinct species**, or with the **physical conditions** of life.

C. Darwin, Origin of the Species
As quoted in Ricklefs (1993)

Factors Influencing Populations

Physical Factors

- e.g. temperature, salinity
- **density independent**

Intraspecific Interactions

- Exploitative Competition
 - no direct interaction
 - resource mediated

- Interference Competition
 - direct interaction

density dependent

Interspecific Interactions

(Multiple State Variables)

Question: What regulates population growth?

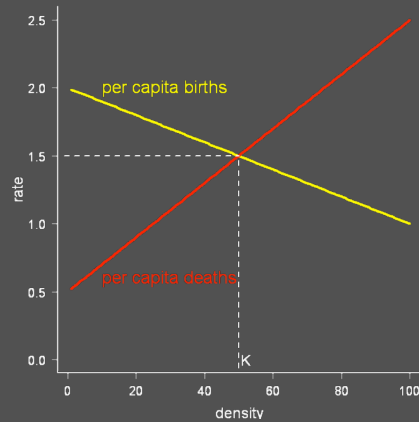
Negative Feedback from a population's **density** onto its growth, reproduction, and survivorship

density dependence
effects that influence a population in proportion to its density

relaxing assumption that *b* and *d* are constant

$$b, d = f(N) \quad b' = b - aN$$

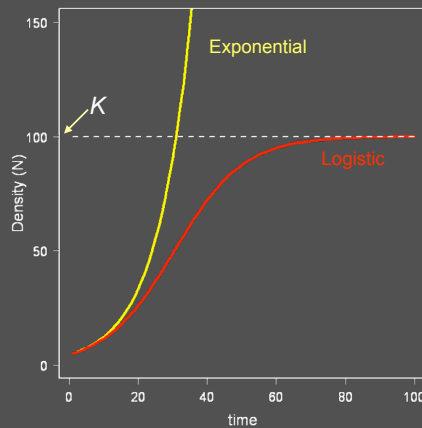
$$d' = d - cN$$



This is implicit in the carrying capacity concept in the **logistic growth model**

Logistic Growth Model

$$\frac{dN}{dt} = rN * \left(1 - \frac{N}{K}\right)$$



Carrying Capacity:
maximum sustainable population size for a given environment

K is a function of **resources** essential for growth and reproduction

Sketch Forrester Diagram

Population Projections: Analytical Solution of Logistic Model

As with the analytical solution to the exponential growth model, this solution can be used to **project** the population size in the future.

$$N_t = \frac{K}{1 + [(K - N_0)/N_0] e^{-rt}}$$

Initial Value Problem

Can you explain how was this equation derived?

(hint see Gotelli p. 29)

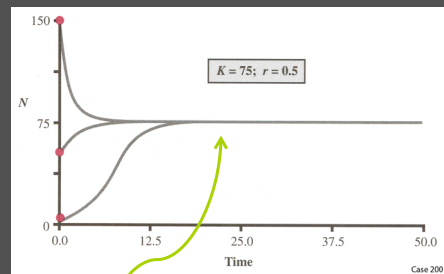
How is this different from solving the differential equation using numerical estimation algorithms (Euler or Isoda)?

Model Analysis: Equilibriums

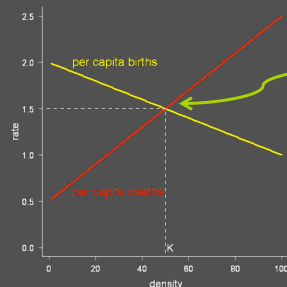
What are the possible dynamics of the model?

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right)$$

$$0 = rN \left(1 - \frac{N}{K} \right)$$



Like the exponential, $r = 0$ and $N = 0$ are equilibriums. When else?



$N = K$

Stable equilibrium

See Gotelli Appendix
for more detail

Model Analysis: Per Capita Growth Rate

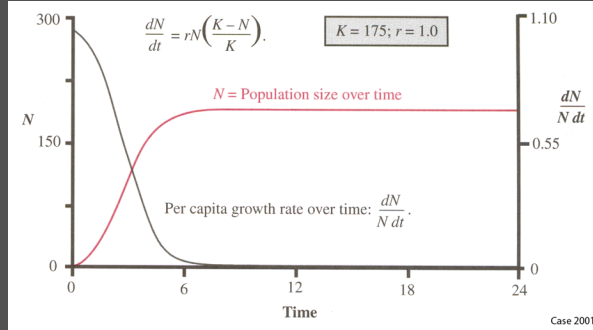
$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right)$$

Can be written as

$$\frac{dN}{dt} = rN \left(\frac{K-N}{K} \right)$$

Per capita growth rate is

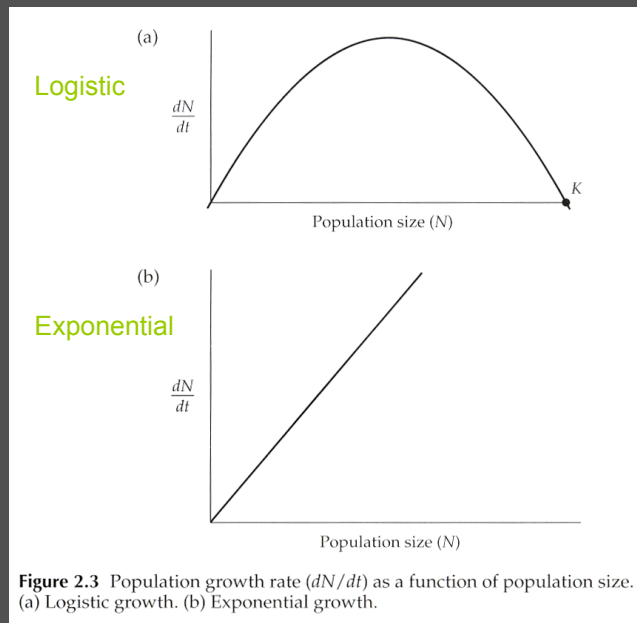
$$\frac{1}{N} \frac{dN}{dt} = r \left(\frac{K-N}{K} \right)$$



$$\left[\begin{array}{l} \text{The rate of} \\ \text{increase of the} \\ \text{population} \end{array} \right] = \left[\begin{array}{l} \text{the maximum rate of} \\ \text{population growth} \\ \text{per capita, } r \end{array} \right] \left[\begin{array}{l} \text{the number of} \\ \text{individuals, } N \end{array} \right] \left[\begin{array}{l} \text{the unutilized} \\ \text{opportunity for} \\ \text{population growth} \end{array} \right]$$

As the population increases in size, the individuals start to "interfere" with the other individuals' activities, causing the population growth rate to decline.

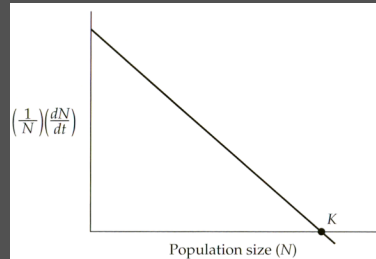
Growth Rate Comparisons



Logistic Model Assumptions (additional)

Assumes

- (1) **constant carrying capacity**
 - resource availability does not change through time.
 - alternatives = stochastic model, periodic variation, refuge
- (2) **linear density dependence**
- (3) **maximum growth rate occurs when $N = 0$.**
- (4) **density dependence** operates equally on all components of r (b, d, e, i)
- (4) **increasing density is always detrimental**
 - alternative = Allee Effect



Extending the Model: Alternative Control Functions

We can rewrite the density dependent growth model in a more general form as

$$\frac{dN}{dt} = rN * f(N)$$

In the classic logistic model

$$f(N) = \left(1 - \frac{N}{k}\right)$$

Sometimes it is useful to consider alternative functional forms.

- guided by **data** or **alternative hypotheses** about the form
- can also include conditions such **refuges** and the **allee** effect

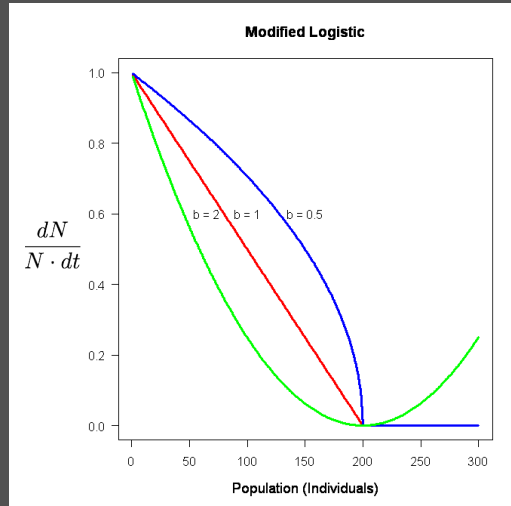
Modified Logistic: Non-Linear density dependence

What if your data suggest that the per capita growth rate is not linear?

$$\frac{dN}{N \cdot dt} = \left[r \left(1 - \frac{N}{K} \right)^b \right]_+$$

Here we added two types of non-linearities

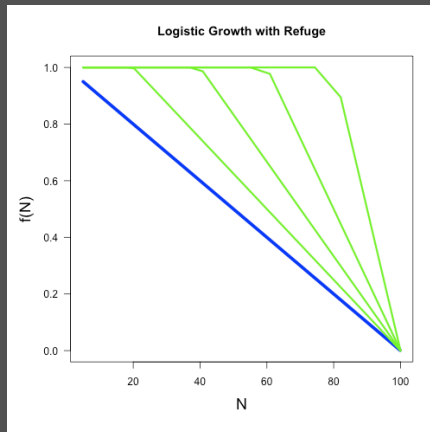
1. Introduced a threshold (+)
Comment on control technique (positive)
 This may or may not be desired, depending on use
2. Added a shape parameter (b)



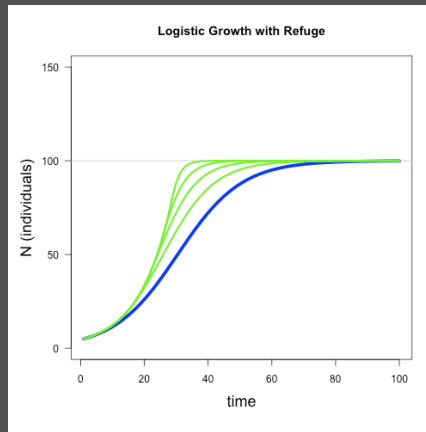
Modified Logistic: Adding a Refuge

$$\frac{dN}{dt} = rN * f(N) \quad f(N) = \left[1 - \left(\frac{N - \alpha}{K - \alpha} \right) \right]_+$$

Control Function Plot



Model Solution Plot



Allee

We will consider this another day.

What do you think it will look like?

See if you can sketch out what you think the control function behavior should look like.

Alternative Functional Forms of Growth Rate Controls

Density *independent* control; external resource control

Monod Equation

(aka Michaelis-Menton)

$$\frac{R}{R + k}$$

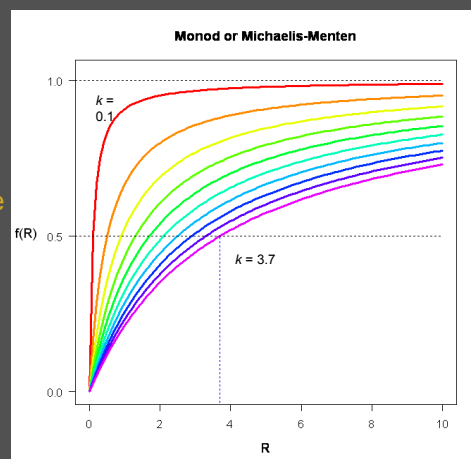
Where
 R = the resource concentration
 k = $\frac{1}{2}$ saturation constant

Control Function Approach –
 Modified Growth Rate

$$\frac{1}{N} \frac{dN}{dt} = r * f(R) = r \left(\frac{R}{R + k} \right)$$

Disadvantages

1. Never recover maximum growth
2. Limited shape
3. Always begins at $R=0$
4. Applies to all parts of r equally
5. Not density-dependent control



Many types of possible functions

Summary

- Density dependence controls population growth
- Logistic function is a classic way to model density dependence in populations
- Describe the assumptions of the logistic equation
- Alternative functional forms
 - Non-linear logistic
 - Refuge form of logistic
 - Adding +constraints (more on this later)
 - Monod Function