MA 331

Differential Equations for the Life Sciences

Fall 2018

Lecture 3: Population Models

Population Models

Simplest model: exponential growth $\frac{dN}{dt} = rN$

Growth rate proportional to population size

Four names for r : (1) "growth constant", (2) "intrinsic growth rate"

I don't like this name, but ecologists often call it this

Important: Growth rate and growth constant mean different things

$r = \frac{\frac{dN}{dt}}{N}$ (3) Growth rate **per individual** : (4) "**per-capita** growth rate"

Exponential growth model assumes that the per-capita growth rate is constant; in particular, it doesn't depend on population size

Breaking down " *r* "

$$\frac{dN}{dt} = B - D$$ *B*, *D* are birth and death rates

Assume that birth rate is proportional to population size

$B = bN$ so $b = B/N$ *b* is the per-capita birth rate

Assume that death rate is proportional to population size

$D = dN$ so $d = D/N$ *d* is the per-capita death rate

Then:

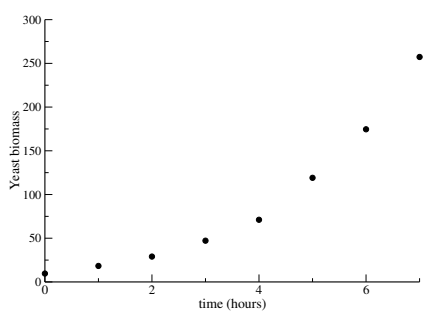
$$\frac{dN}{dt} = bN - dN = rN \quad \text{with} \quad r = b - d$$

r is the difference between per-capita birth and death rates

The exponential growth model arises if we assume constant per-capita birth and death rates

How Well Does Exponential Growth Model Work?

Yeast growth experiment (Carlson, 1913)

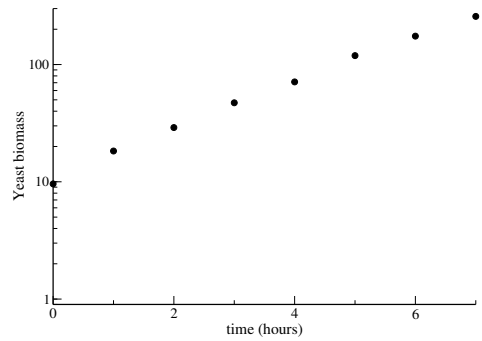


Data from first 7 hours look exponential.

Not so easy to say for sure. How can we be more certain?

How Well Does Exponential Growth Model Work?

Easier to identify exponential growth on a "semi-log" plot
(either log scale on vertical axis or plot ln(data) vs time)



Straight line on a semi-log plot indicates exponential growth

Interlude: theory behind semi-log plot

Suppose $N = N_0 e^{rt}$

Take natural logs of both sides of this equation

$$\ln N = \ln\left(N_0 e^{rt}\right)$$

$$\ln N = \ln N_0 + \ln\left(e^{rt}\right)$$

$$\ln N = \ln N_0 + rt$$

Plot ln N (vertical) vs t (horizontal), so $y = \ln N$ and $x = t$

$$y = \ln N_0 + rx$$

Straight line, slope r and y-intercept $\ln(N_0)$

Semi-log plot gives us a way to estimate the growth constant (per-capita growth rate)

How Well Does Exponential Growth Model Work?

Problem with exponential growth as a population model?

Unbounded growth… and ever faster growth

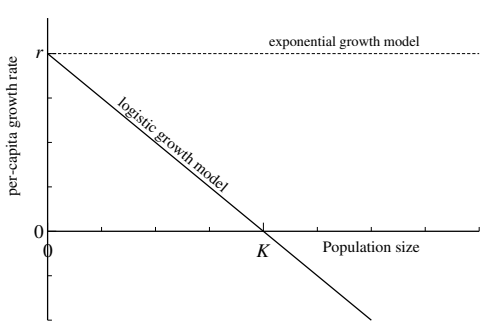
Cannot be realistic: finite resources (food, space, …)

Might expect per-capita growth rate to decrease as *N* increases, even becoming negative when *N* is "too large"

Logistic Growth Model

Makes the simplest assumption about per-capita growth rate consistent with the idea that pcgr decreases with *N* and eventually becomes negative

Assume that per-capita growth rate decreases linearly with *N* :



Take the per-capita growth rate to equal *r* when *N* = 0

(same as exponential growth model)

Let *K* be the population size when pcgr equals zero

$$pcgr = r - \frac{r}{K}N$$

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

Logistic Growth Model $pcgr = r\left(1 - \frac{N}{K}\right)$

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

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

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

Per-capita growth rate decreases with *N*, rather than remaining constant

Ecologists call this **"density-dependent"** growth

Can simplify notation, converting to our earlier notation:

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

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

Write $y = N$, $a = K$, $k = r/K$: $\frac{dy}{dt} = k\,y\left(a-y\right)$

Back to Yeast…

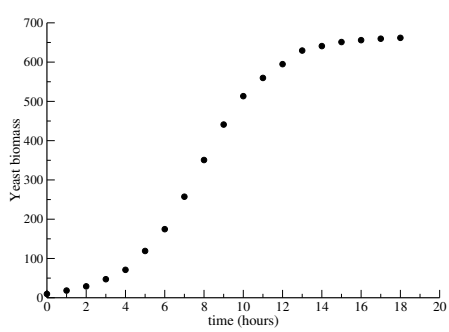
Problem with exponential growth: as a population model?

Unbounded growth… and ever faster growth

Cannot be realistic: finite resources (food, space, …)

Might expect per-capita growth rate to decrease as *N* increases

What happens to the yeast population?

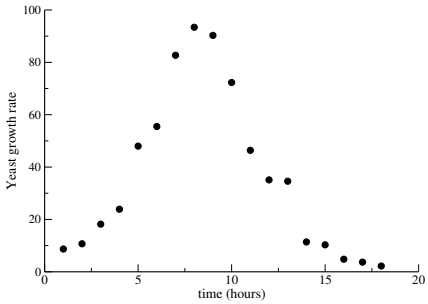


Over a longer timeframe, growth slows

Population appears to approach a plateau (equilibrium)

What can we say about birth and death rate at equilibrium?

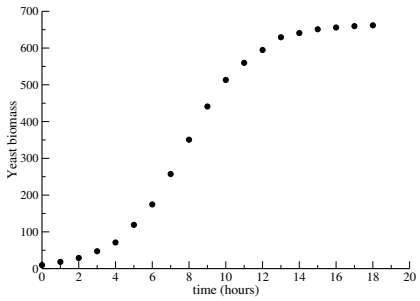
Yeast growth rate



Over time, growth rate first increases, then decreases

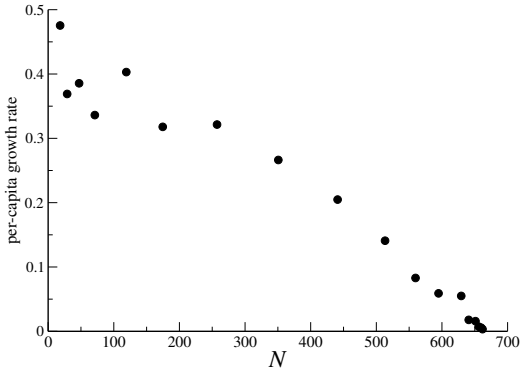
Most rapid growth occurs when?

Inflection point on population/time curve



Yeast growth rate

What does per-capita growth rate look like?



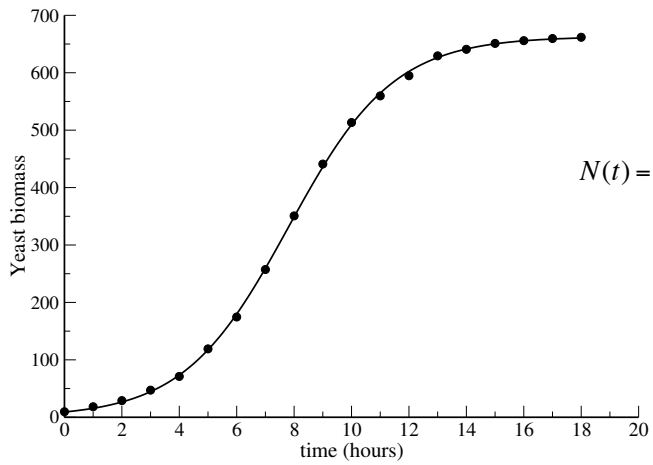
Per-capita growth rate decreases as *N* increases…

and not so far away from being a linear decrease

Remember: $pcgr = r - \frac{r}{K}N$

Gives us a way to estimate *r* and *K* : fit a straight line to per-capita growth rate

Back to Yeast…



$$N(t) = \frac{663.02}{1 + 71.576\, e^{-0.5470t}}$$

Logistic growth model gives a very good fit to this data

Other Growth Models

Logistic growth model is just a model (or approximation) – not a "law"

Many other growth models, including the Gompertz model:

$$\frac{dN}{dt} = \alpha \ln\left(\frac{K}{N}\right) N \qquad \text{solution:} \quad N(t) = K\left(\frac{N(0)}{K}\right)^{e^{-\alpha t}}$$

(double exponential)

(I don't expect you to remember either of these two)

Von Foerster model (1960) $\frac{dN}{dt} = \alpha_0 N^{1/k}$

If $k < 1$, the growth rate in this model grows faster than that of the exponential growth model

- bizarrely, the population will reach infinity in a finite amount of time
- Von Foerster et al. (1960) measured $k = 0.990$…
  and predicted Doomsday would be Friday, November 13th 2026

Allee Effect Model

Logistic growth model assumed that the largest per-capita growth rate occurs for small population sizes

This isn't a good assumption for all populations: some populations do worse when the population size is small

Why?

Difficulty in finding mates
Difficulty in avoiding predators
More difficult to find/handle food

(Animal herds, fish shoaling, …)

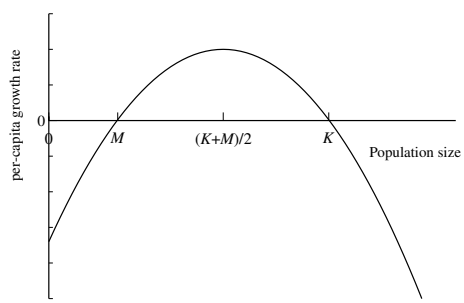
Allee effect: per-capita growth rate declines as population gets "too small", maybe even becoming negative

Some ecologists talk about "weak Allee effect": decline in pcgr for small *N* vs "strong Allee effect": pcgr becomes negative for small *N*

I use "Allee effect" to mean that the per-capita growth rate becomes negative

Allee Effect Model **("strong Allee effect" model)**

Per-capita growth rate is negative when *N* is small



Simplest function to model this: $pcgr = a(M-N)(N-K)$ with $0 < M < K$

Allee effect model: $\frac{dN}{dt} = a(M-N)(N-K)N$ with $0 < M < K$, $a > 0$

Allee Effect Model

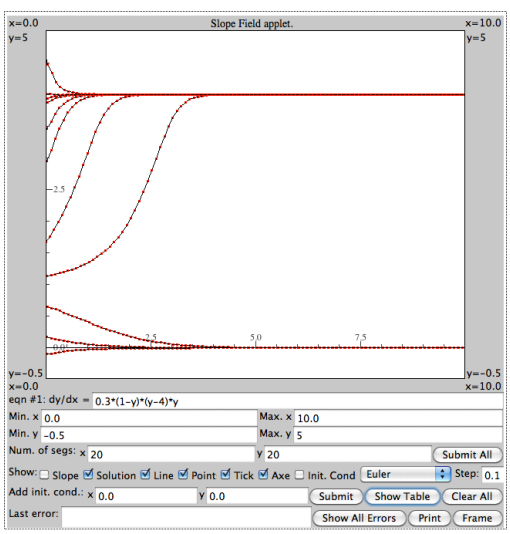
$$\frac{dN}{dt} = a(M-N)(N-K)N$$

Explore behavior using numerical solver (see "Resources" on course website)

Allee Effect Model

$$\frac{dN}{dt} = a(M-N)(N-K)N$$

Slope Field Calculator



I chose a = 0.3, M = 1, K = 4

Equilibria at N = 0, 1 and 4

If $N(0) > 1$, then N approaches 4 in the long run

If $N(0) < 1$, then N approaches 0 in the long run - extinction

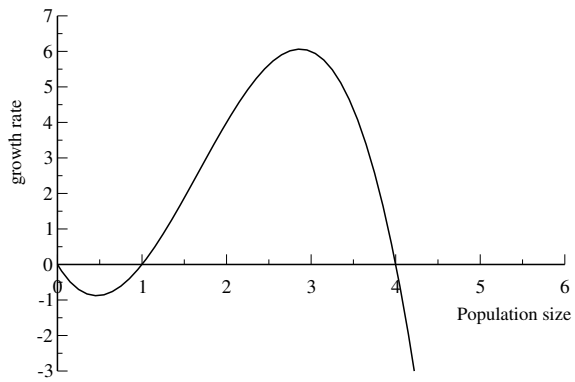
$N(0) = M$ represents a threshold for this model
"minimum viable population"

Stability of equilibria?

Can We Understand the Behavior of the Allee Effect Model?

Plot growth rate, dN/dt, as a function of population size N

$$\frac{dN}{dt} = a(M-N)(N-K)N$$



Growth rate is zero when N is 0, 1 or 4 (i.e. 0, M or K)
- equilibria

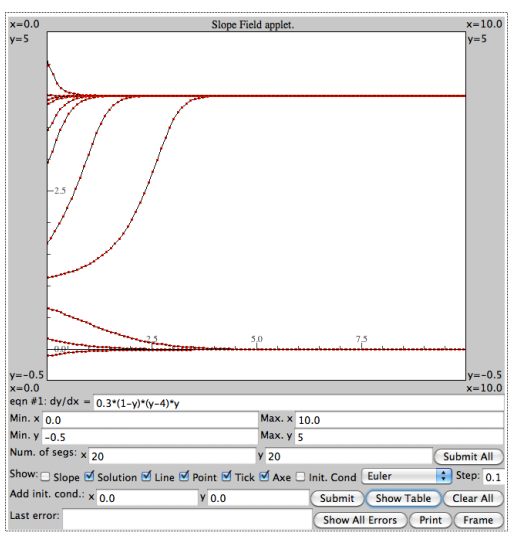
Growth rate is negative when N is above 4 (i.e. above K)
- population will decrease

Growth rate is negative when N is below 1 (i.e. below M) but above 0
- population will decrease

Growth rate is positive when N is between 1 and 4 (i.e. between M and K)
- population will increase

Can We Understand the Behavior of the Allee Effect Model?

Slope Field Calculator



Verbal argument that considers when growth rate is positive or negative explains the qualitative features of the Allee effect solution curves

Does a little better than that: can we understand where the inflection point is on (some) solution curves?

Over the next few classes, we will formalize this graphical argument and learn how to obtain numerical solutions