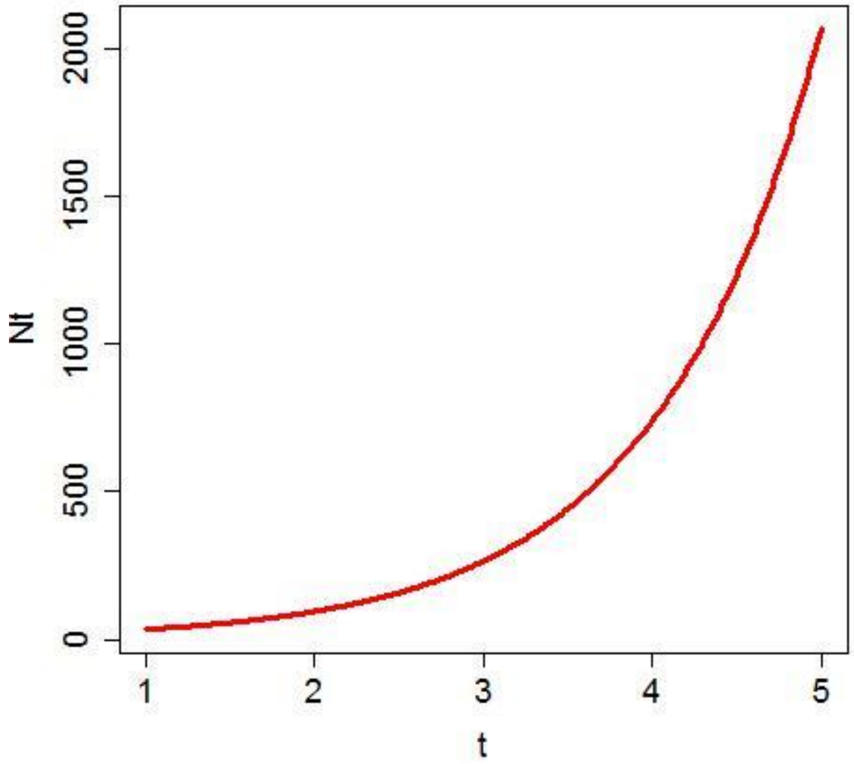
BIOL 410 Population and Community Ecology

Density-dependent growth 1

Exponential growth

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




```r
# Model 6, Exponential growth
t <- seq(1,5,0.01)
tn <- seq(1,length(t),1)
Nt <- rep(NA,length(t))
r <- log(2.8)
N0 <- 12
Nt[tn] <- N0*exp(r*t)
```

Deterministic model

Exponential growth

Dennis et al. 1991

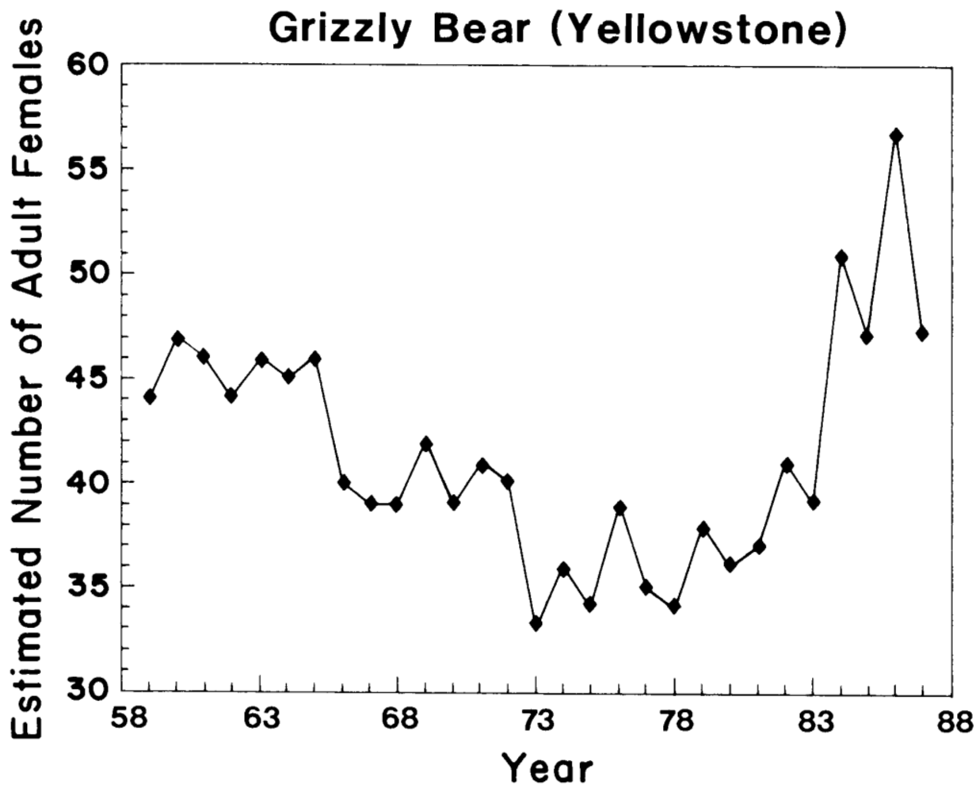
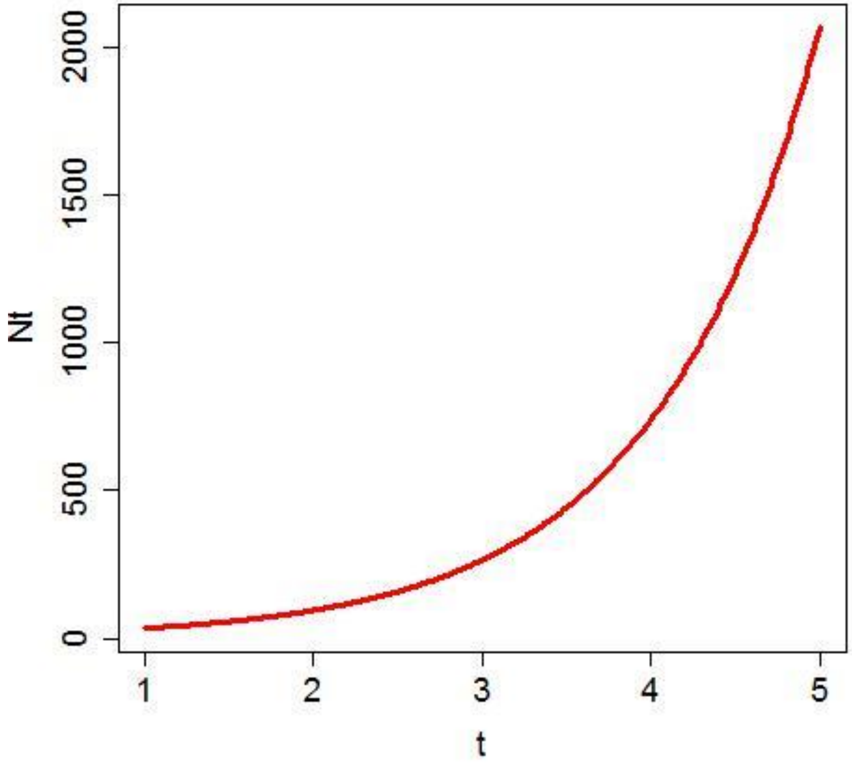


FIG. 5. Estimated number of adult females in the Yellowstone National Park grizzly bear population, 1959–1987. Data, listed by Eberhardt et al. (1986) and supplemented by recent figures, consist of a 3-yr moving sum of the yearly number of adult females seen with cubs.

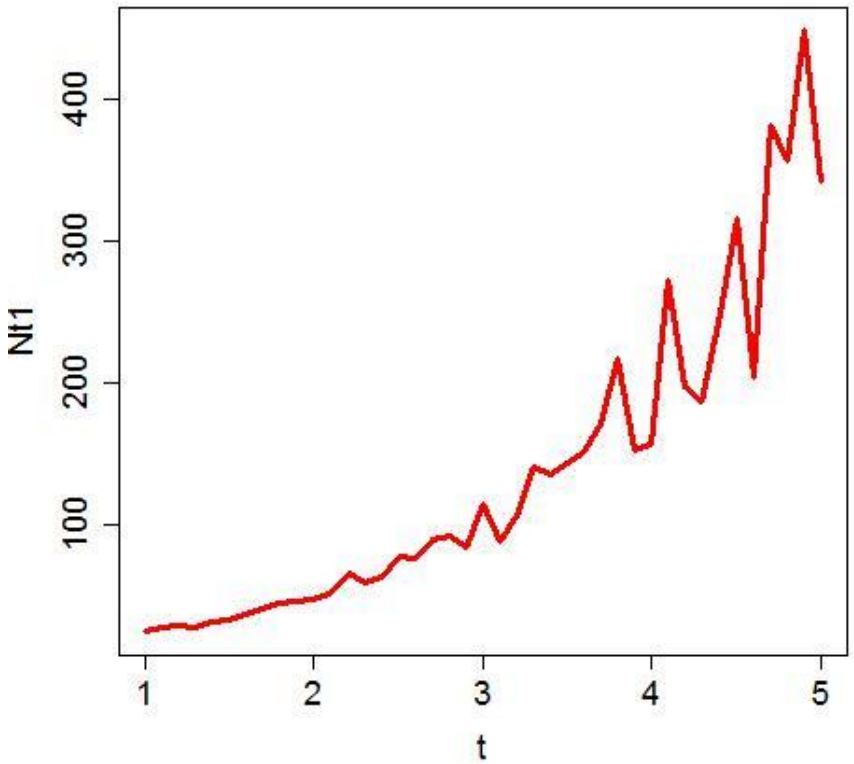
Exponential growth

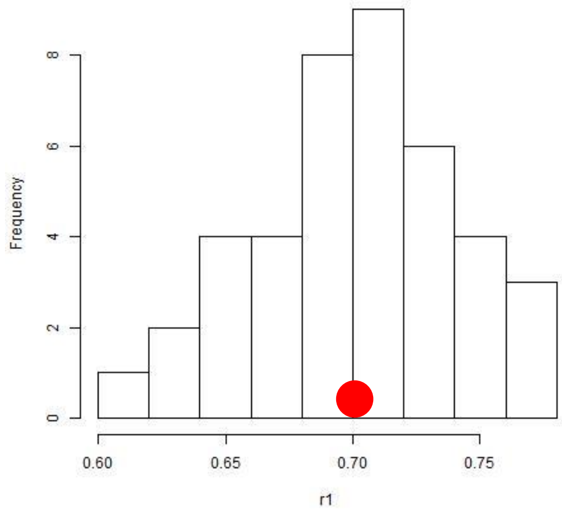
$$N_t = N_0 e^{rt}$$




```
# Model 6, Exponential growth
t <- seq(1,5,0.01)
tn <- seq(1,length(t),1)
Nt <- rep(NA,length(t))

r <- log(2.8)
N0 <- 12
Nt[tn] <- N0*exp(r*t)
```

Stochastic population growth

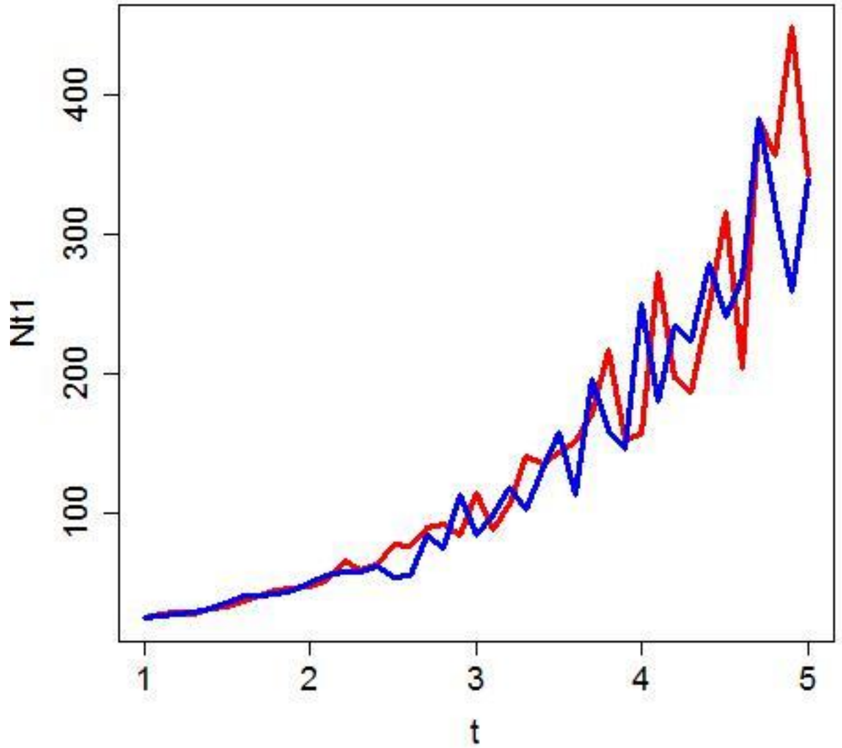




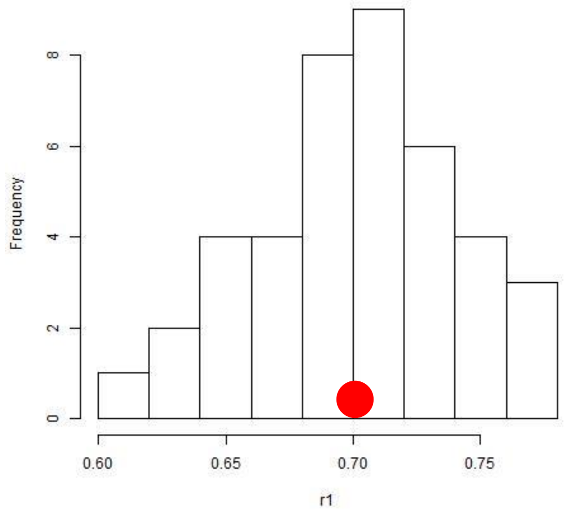
Normal distribution

```
# Model 8, stochastic Exponential growth
t <- seq(1,5,0.1)
tn <- seq(1,length(t),1)
Nt1 <- rep(NA,length(t))
Nt2 <- rep(NA,length(t))

r1 <- rnorm(length(t),log(2),0.04)
r2 <- rnorm(length(t),log(2),0.04)
N0 <- 12
Nt1[tn] <- N0*exp(r1[tn]*t)
Nt2[tn] <- N0*exp(r2[tn]*t)
```

Stochastic population growth

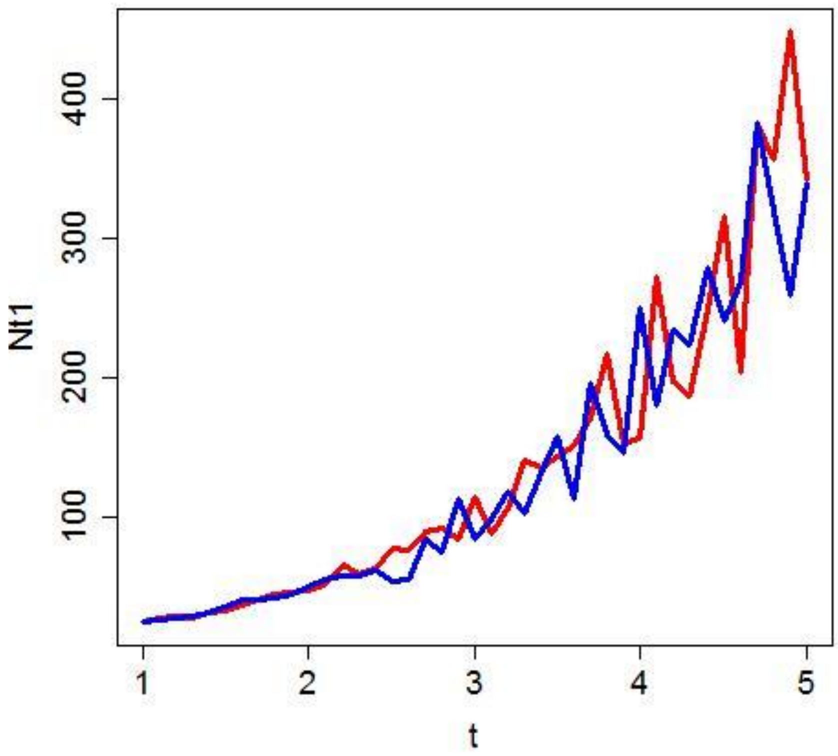


Random




```
# Model 8, stochastic Exponential growth
t <- seq(1,5,0.1)
tn <- seq(1,length(t),1)
Nt1 <- rep(NA,length(t))
Nt2 <- rep(NA,length(t))

r1 <- rnorm(length(t),log(2),0.04)
r2 <- rnorm(length(t),log(2),0.04)
N0 <- 12
Nt1[tn] <- N0*exp(r1[tn]*t)
Nt2[tn] <- N0*exp(r2[tn]*t)
```

Why include stochasticity?



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

Density dependence

Objectives

- Density dependence
- Carrying capacity
- Negative and positive density dependence
- Time lags
- Cyclic populations
- Oscillations, dampening oscillations

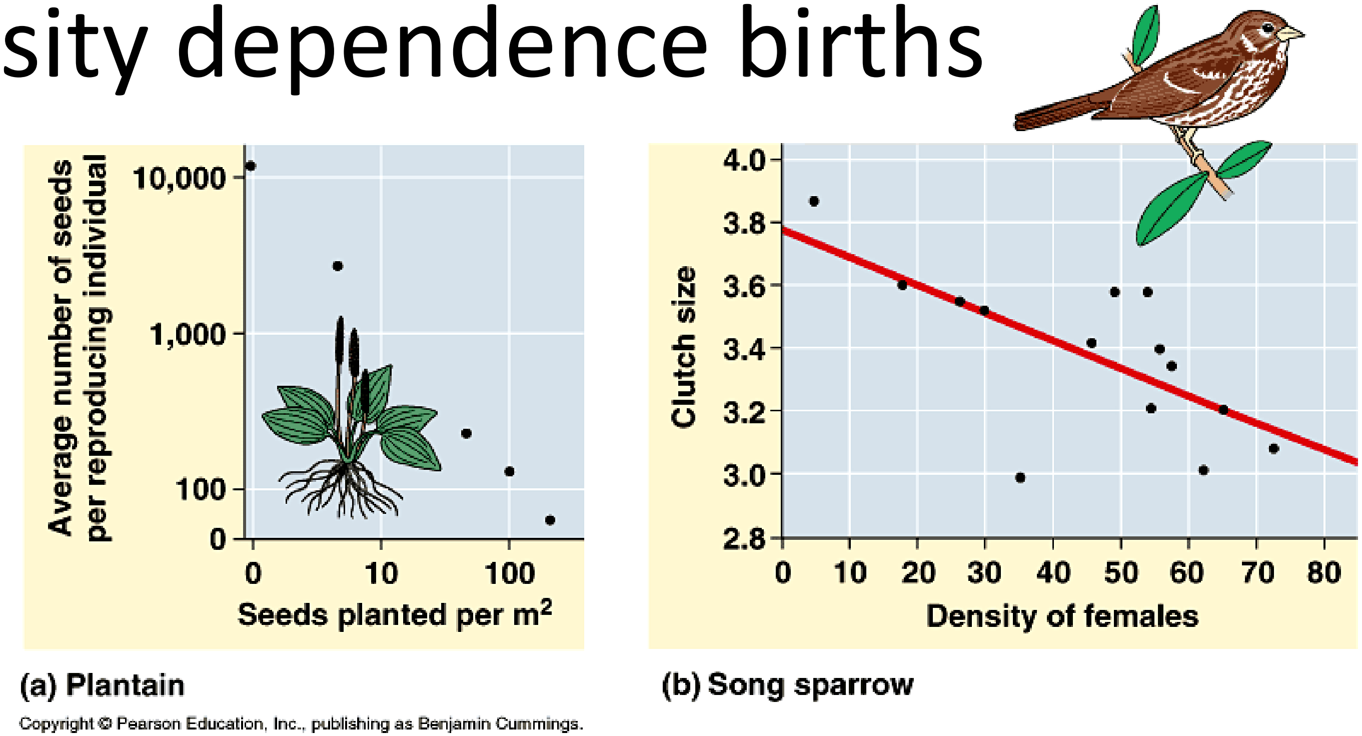
Density dependence

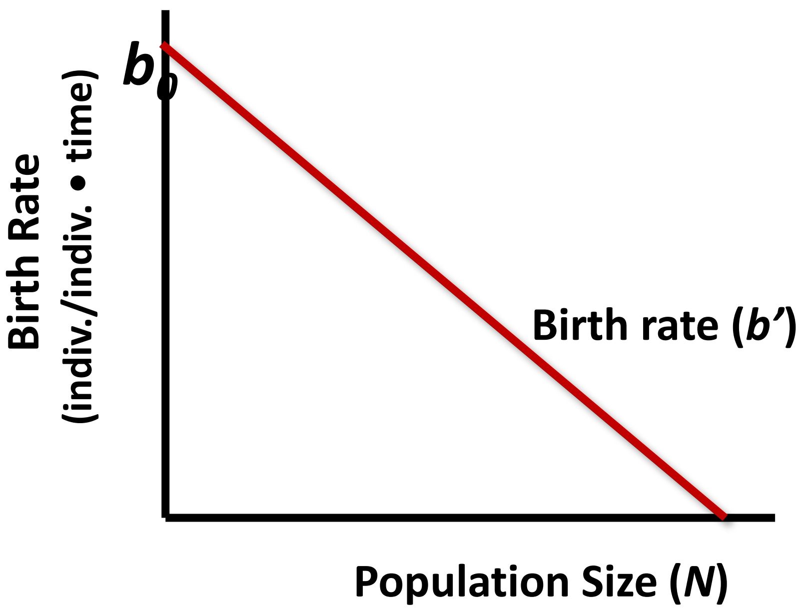
$$N_{t+1} = N_t + b \cdot N_t - m \cdot N_t$$

$$\frac{dN}{dt} = (b - d)N$$

No resource limitation

Density dependence births

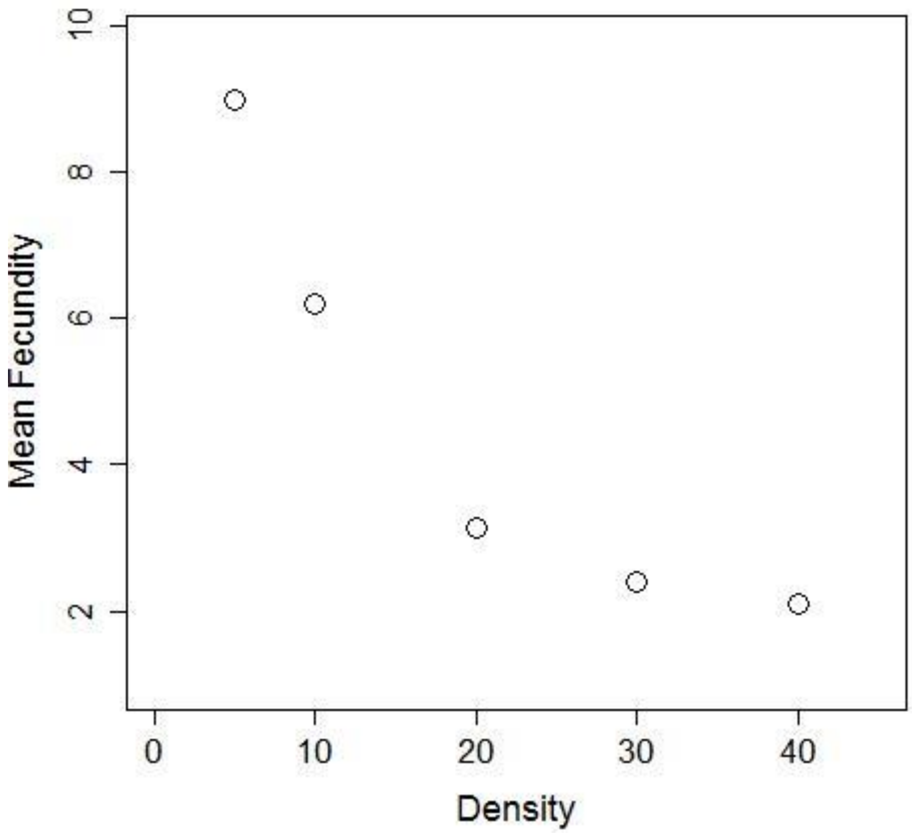




$$\frac{dN}{dt} = (b - d)N$$

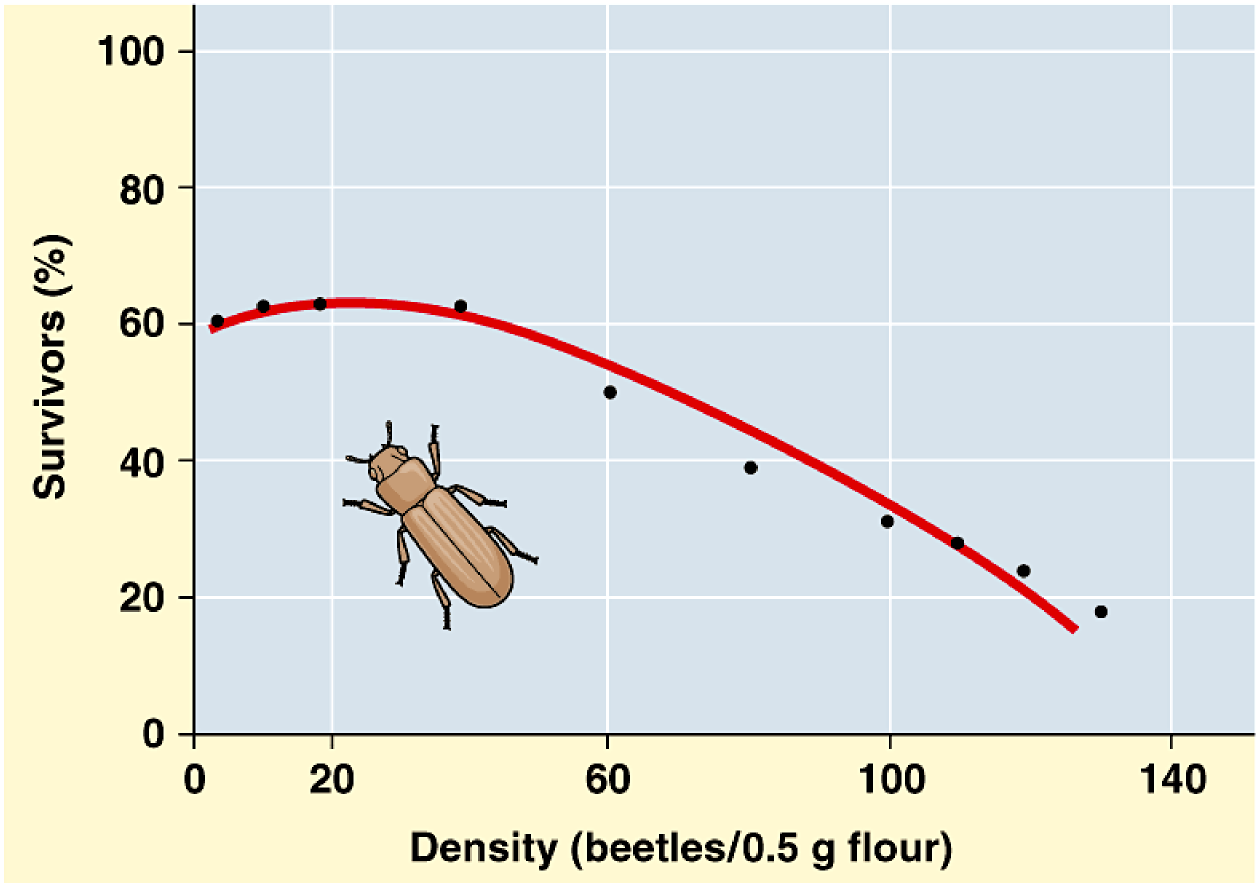
$$\boldsymbol{b' = b - aN}$$

Density dependent births

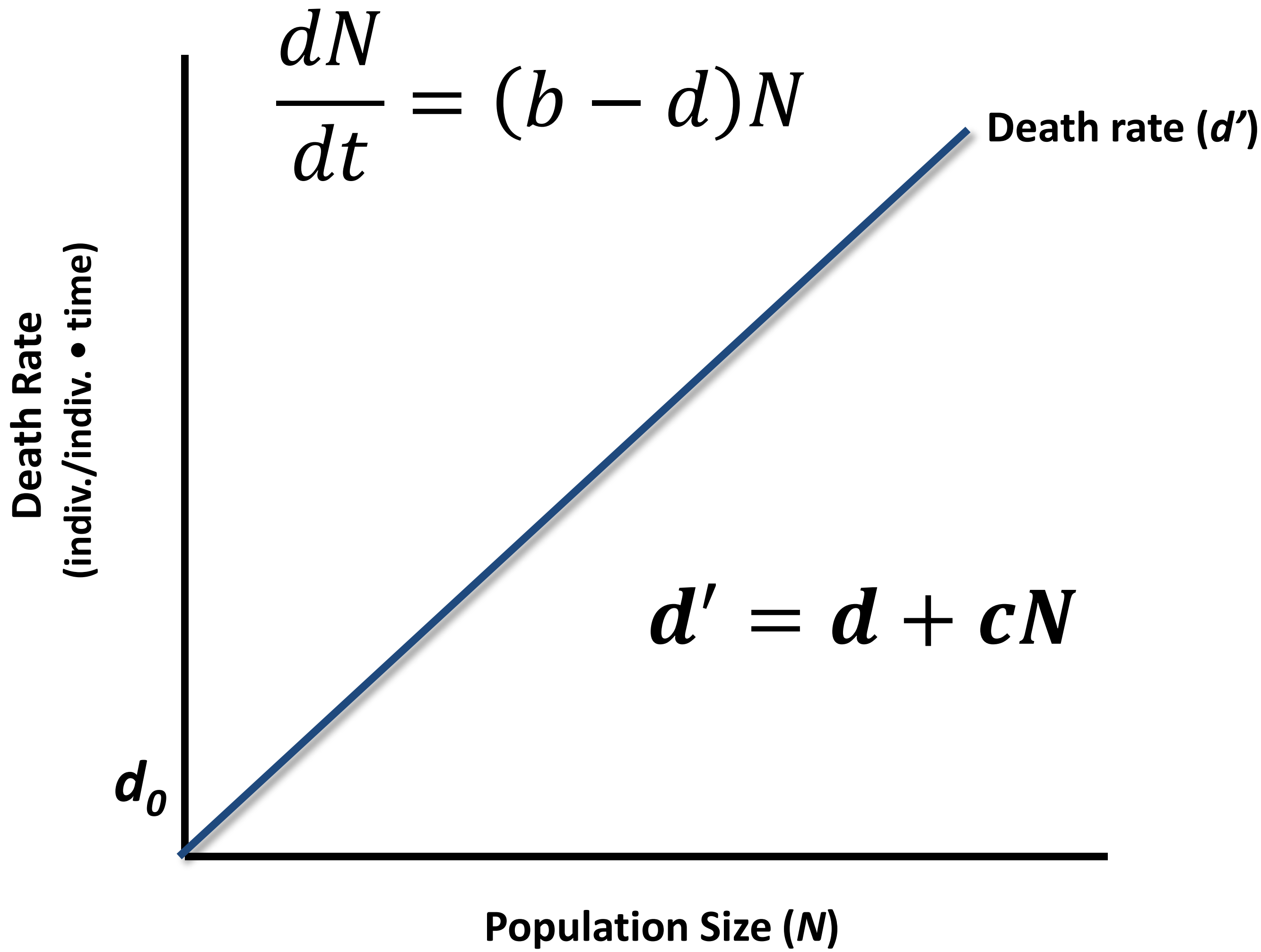


Musculium securis
Fingernail clams
Bergon, Harper and Townsend 1996

Density dependent mortality



Density dependent mortality



Logistic Population Growth

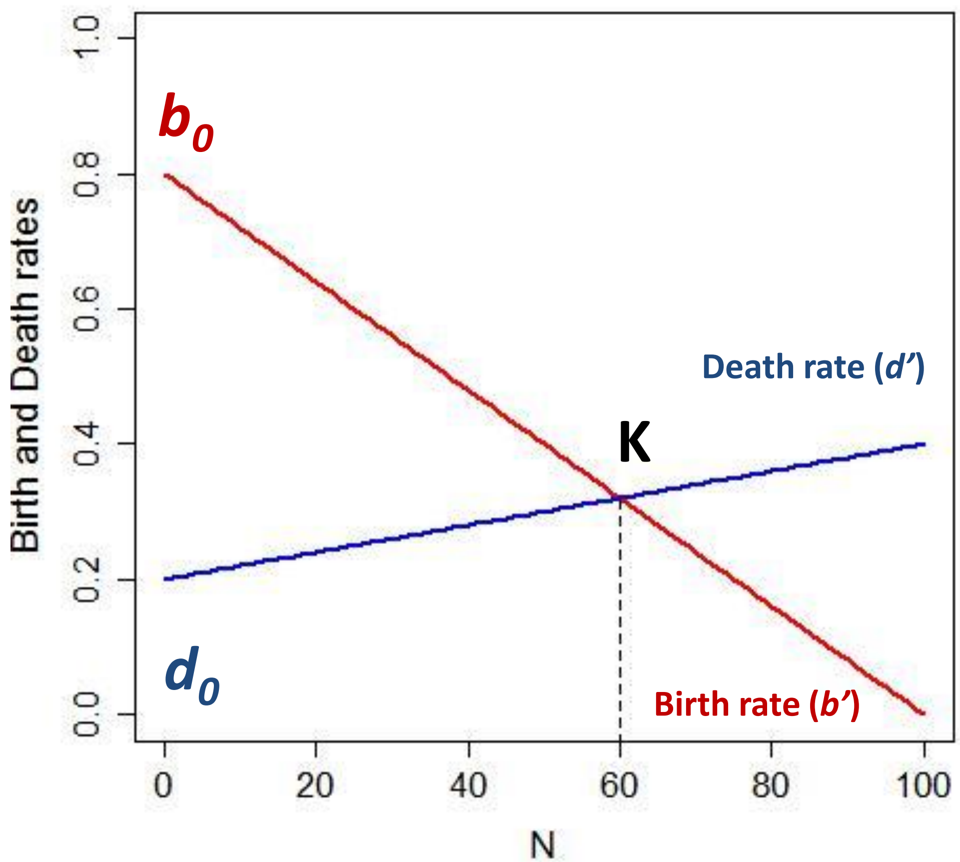
- **Density-dependent Birth (*b'*) & Death Rates (*d'*)**

$$b' = b - aN$$

$$d' = d + cN$$

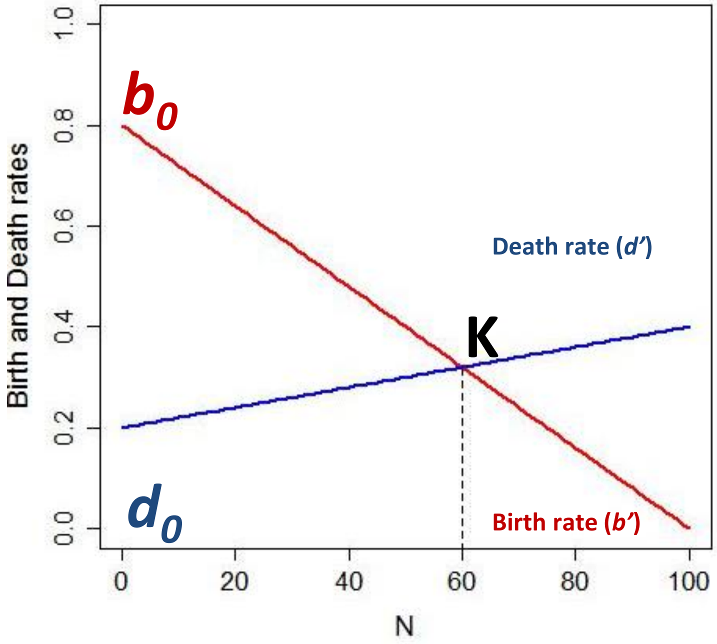
  - ***a*** **&** ***c*** **are slope constants that dictate the *strength* of density-dependence of birth or death rates with increasing population size**
  - **b instantaneous per capita birth rate when resources are unlimited**
  - **d instantaneous per capita mortality rate when resources are unlimited**

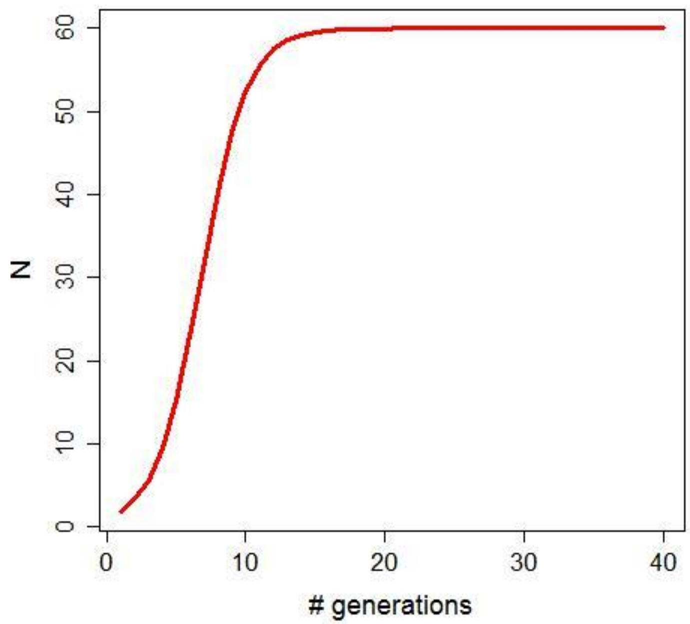
Carrying capacity (K)




```
N <- seq(0,100,1)
t <- seq(1,20,1)
N0 <- 1
b <- 0.8
d <- 0.2

b.alpha <- b/max(N)
d.alpha <- d/max(N)
b.prime <- b - b.alpha*N
d.prime <- d + d.alpha*N
K <- (b - d)/(b.alpha + d.alpha)
bd.intersect <- b - b.alpha*K
```

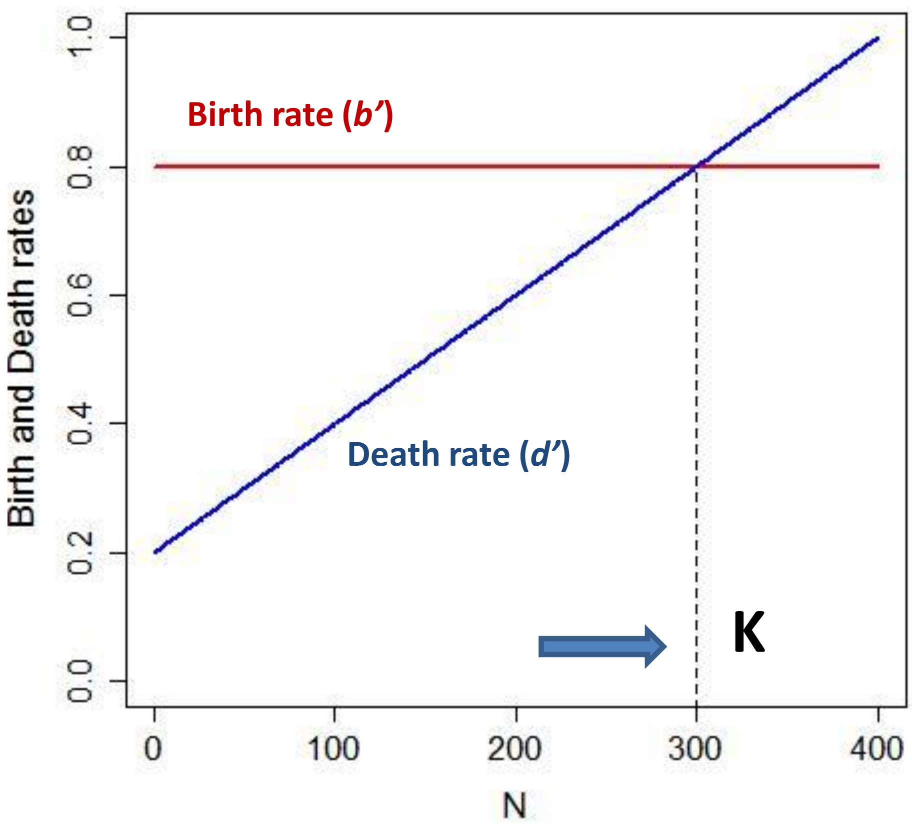
Carrying capacity






```
N <- seq(0,400,1)
t <- seq(1,40,1)
N0 <- 1
b <- 0.8
d <- 0.2

b.alpha <- b/100
d.alpha <- d/100
b.prime <- b - b.alpha*N
d.prime <- d + d.alpha*N
K <- (b - d)/(b.alpha + d.alpha)

r <- (b-d)
Nt <- K/(1+((K-N0)/N0)*exp(-r*t))
```

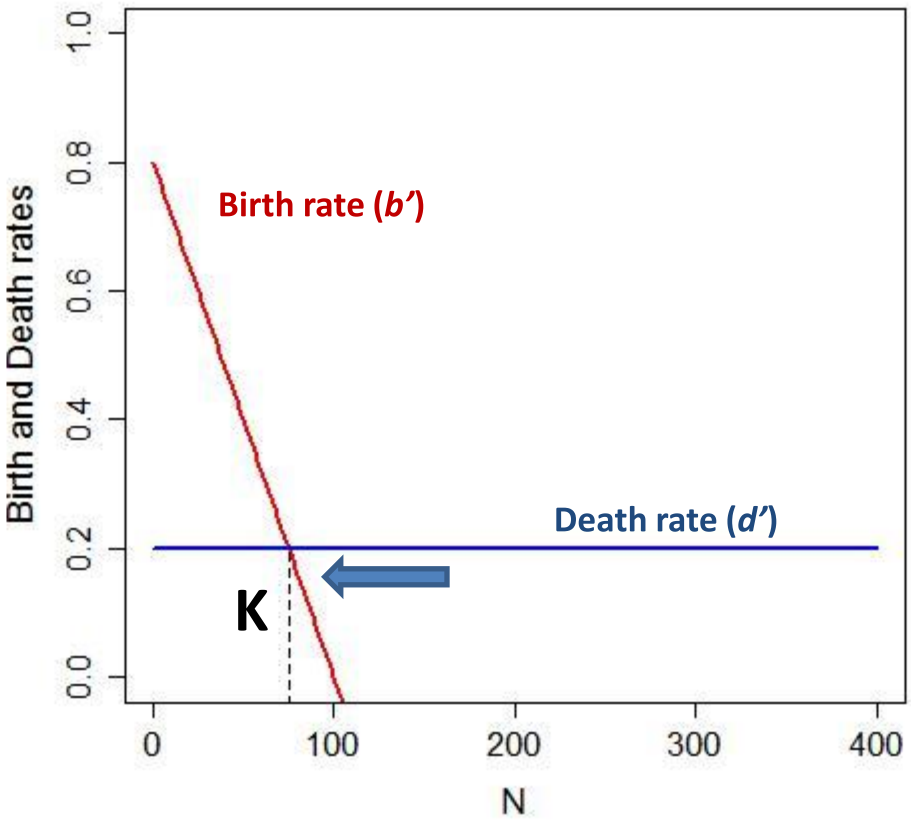
Carrying capacity (K)




```
N <- seq(0,400,1)
t <- seq(1,20,1)
N0 <- 1
b <- 0.8
d <- 0.2

b.alpha <- 0
d.alpha <- d/100
b.prime <- b - b.alpha*N
d.prime <- d + d.alpha*N
K <- (b - d)/(b.alpha + d.alpha)
bd.intersect <- b - b.alpha*K
```

- Density dependent mortality
- Density **independent** births
- K = 300 (previously 60)

Carrying capacity (K)




```
N <- seq(0,400,1)
t <- seq(1,20,1)
N0 <- 1
b <- 0.8
d <- 0.2

b.alpha <- b/100
d.alpha <- 0
b.prime <- b - b.alpha*N
d.prime <- d + d.alpha*N
K <- (b - d)/(b.alpha + d.alpha)
bd.intersect <- b - b.alpha*K
```

- Density **independent** mortality
- Density dependent births
- K = 300 (previously 60)

Logistic Growth Models

- **Integrating Carrying Capacity (K) into growth models**

$$\frac{dN}{dt} = (b - d)N$$

$$\frac{dN}{dt} = (b' - d')N$$

$$b' = b - aN$$

$$d' = d + cN$$

$$\frac{dN}{dt} = [(b - aN) - (d + cN)]\,N$$

Logistic Growth Models

$$\frac{dN}{dt} = [(b - aN) - (d + cN)]\,N$$

$$\frac{dN}{dt} = [(b - d) - (a + c)N]\,N$$

Density dependent constants

Logistic Growth Models

$$\frac{dN}{dt} = [(b-d) - (a+c)N]\,N$$

$$\Downarrow$$

$$\frac{dN}{dt} = \left[\frac{(b-d)}{(b-d)}\right][(b-d) - (a+c)N]\,N$$

$$\Downarrow$$

$$\frac{dN}{dt} = [(b-d)]\left[\frac{(b-d)}{(b-d)} - \frac{(a+c)}{(b-d)}N\right]N$$

$$\Downarrow$$

$$\frac{dN}{dt} = r\left[1 - \frac{(a+c)}{(b-d)}N\right]N$$

define K as $\frac{(\boldsymbol{b}-\boldsymbol{d})}{(\boldsymbol{a}+\boldsymbol{c})}$

Logistic Growth Models

$$\frac{dN}{dt} = r\left[1 - \frac{(a+c)}{(b-d)}N\right]N$$

define K as $\frac{(b-d)}{(a+c)}$

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

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

Exponential Density dependent

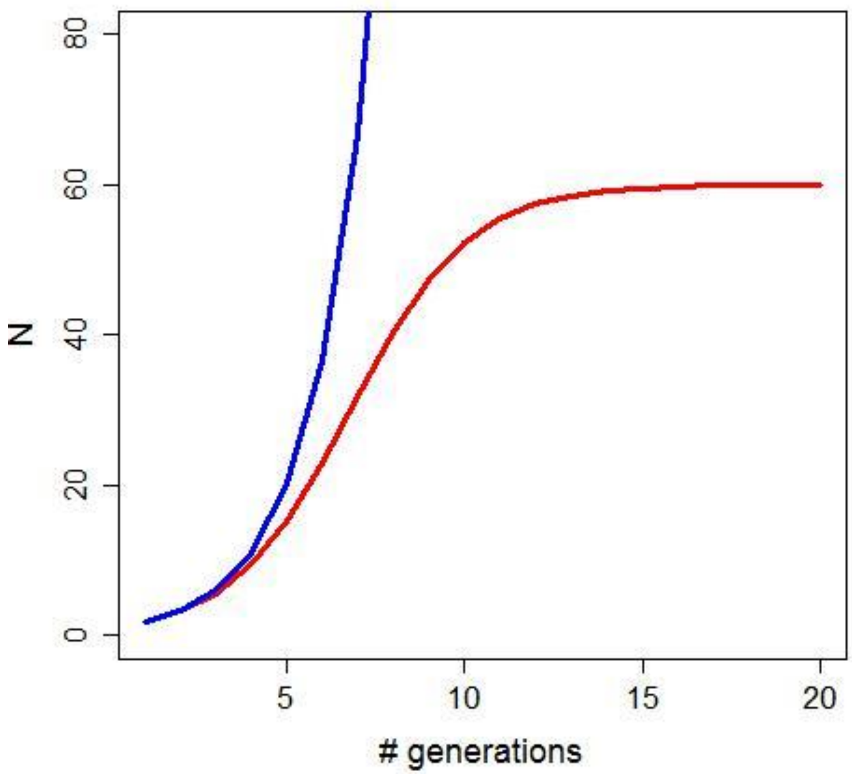
Unused Portion of K

- **Unused portion of the carrying capacity**

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

- **When population size is far below carrying capacity, there is a large unused portion and population growth is high**
  - **K = 1000, N = 5, 0.995**
- **When population size approaches carrying capacity, there is little unused portion remaining, and population growth rate declines**
  - **K = 1000, N = 990, 0.01**

Density independent vs dependent

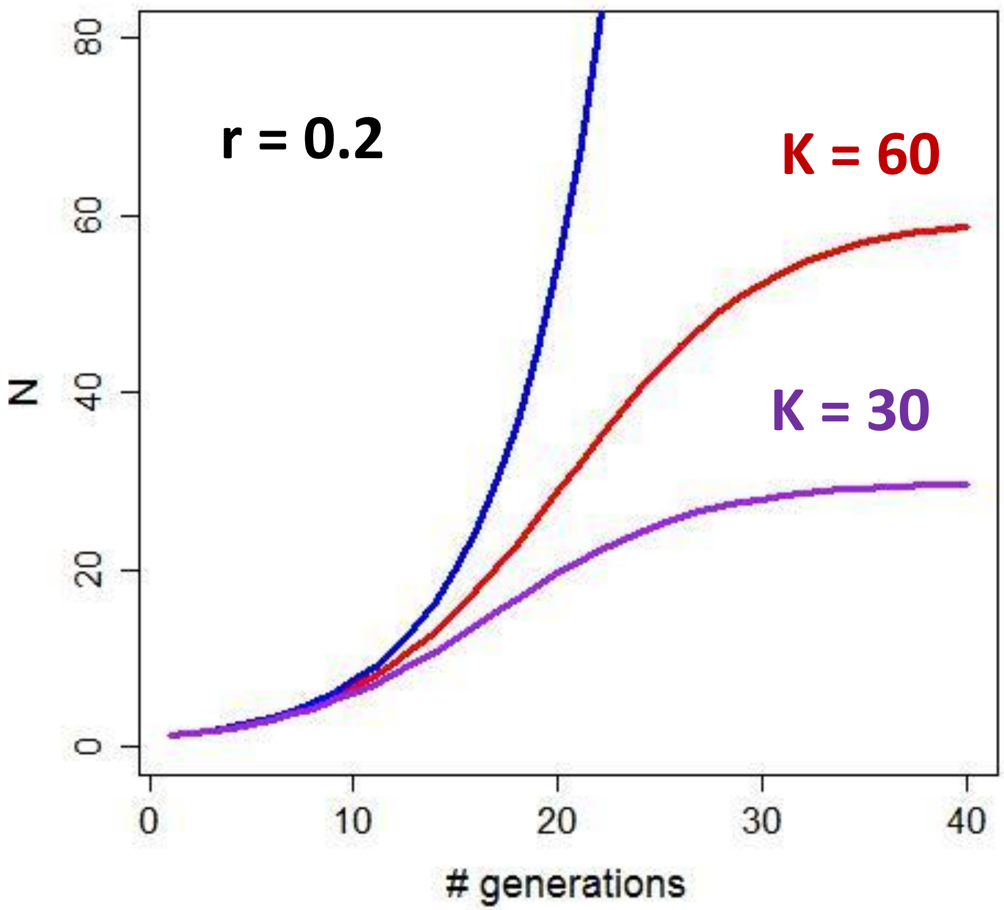



```
N <- seq(0,100,1)
t <- seq(1,20,1)
N0 <- 1
b <- 0.8
d <- 0.2

b.alpha <- b/100
d.alpha <- d/100
b.prime <- b - b.alpha*N
d.prime <- d + d.alpha*N
K <- (b - d)/(b.alpha + d.alpha)
bd.intersect <- b - b.alpha*K

r <- (b-d)
Ntexp <- N0*exp(r*t)
Nt <- K/(1+((K-N0)/N0)*exp(-r*t))
```

$r = 0.6$

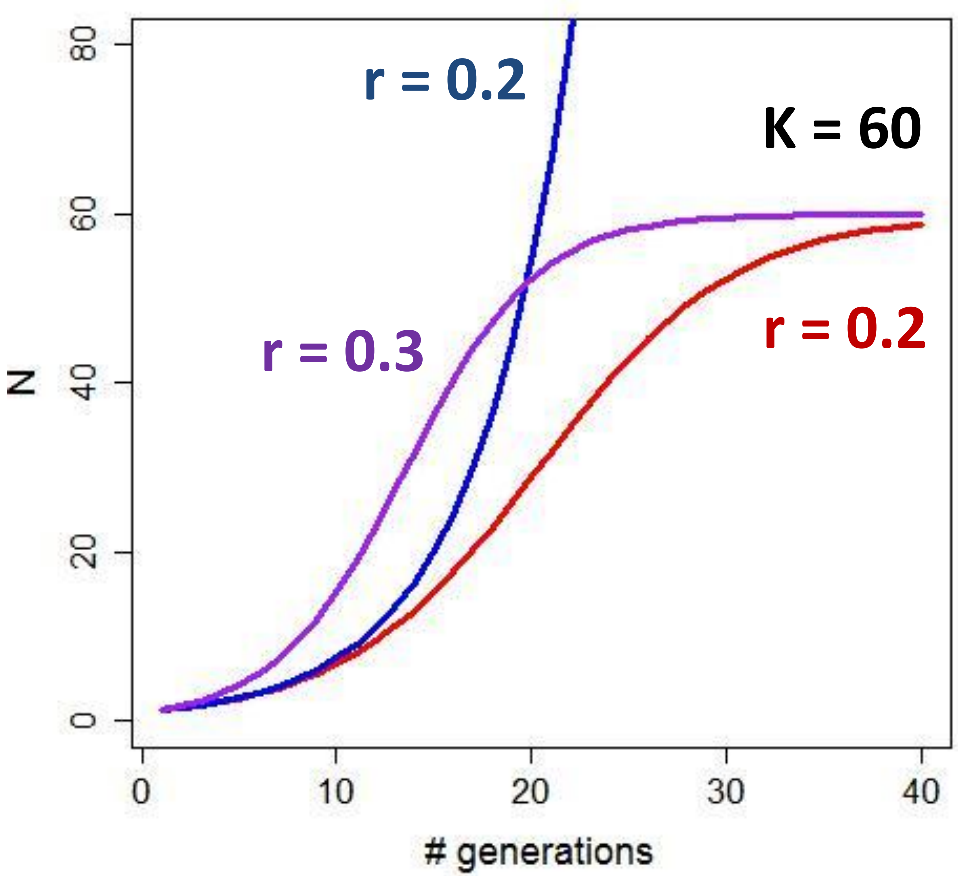
$K = 60$

Logistic population growth



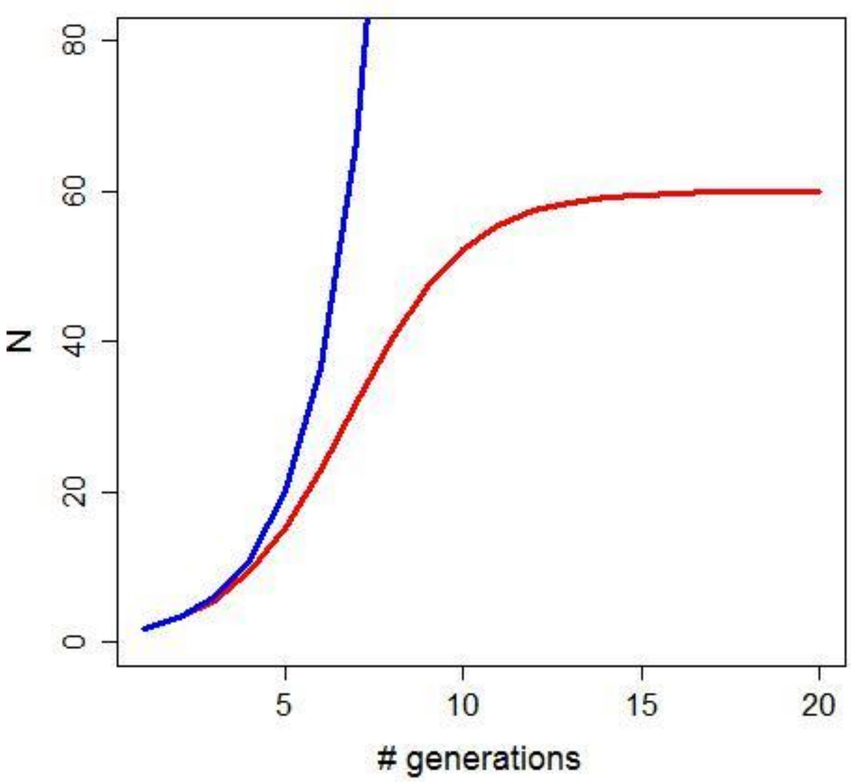

```
N <- seq(0,400,1)
t <- seq(1,40,1)
N0 <- 1
r <- 0.2
K <- 60
K2 <- 30

Ntexp <- N0*exp(r*t)
Nt <- K/(1+((K-N0)/N0)*exp(-r*t))
Nt2 <- K2/(1+((K2-N0)/N0)*exp(-r*t))
```

Logistic population growth




```
N <- seq(0,400,1)
t <- seq(1,40,1)
N0 <- 1
r <- 0.2
r2 <- 0.3
K <- 60
K2 <- 60

Ntexp <- N0*exp(r*t)
Nt <- K/(1+((K-N0)/N0)*exp(-r*t))
Nt2 <- K2/(1+((K2-N0)/N0)*exp(-r2*t))
```

Logistic model integrated



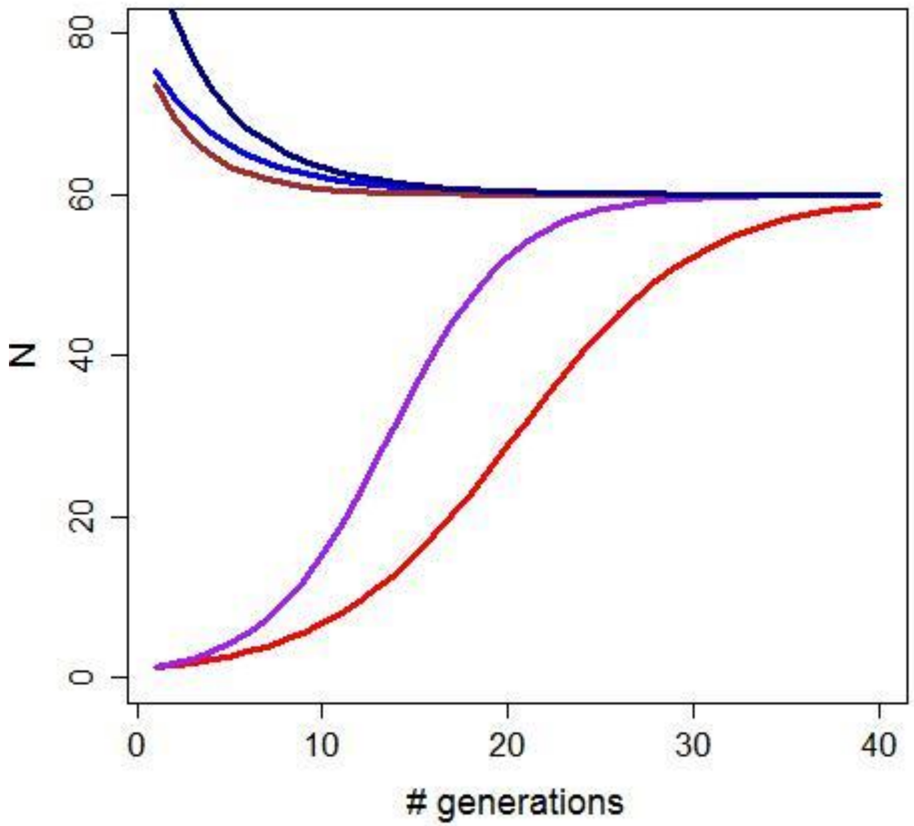
$$\frac{dN}{dt} = rN$$

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

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

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

Logistic population growth



K = 60

r = 0.2, N_0 = 100

r = 0.3, N_0 = 80

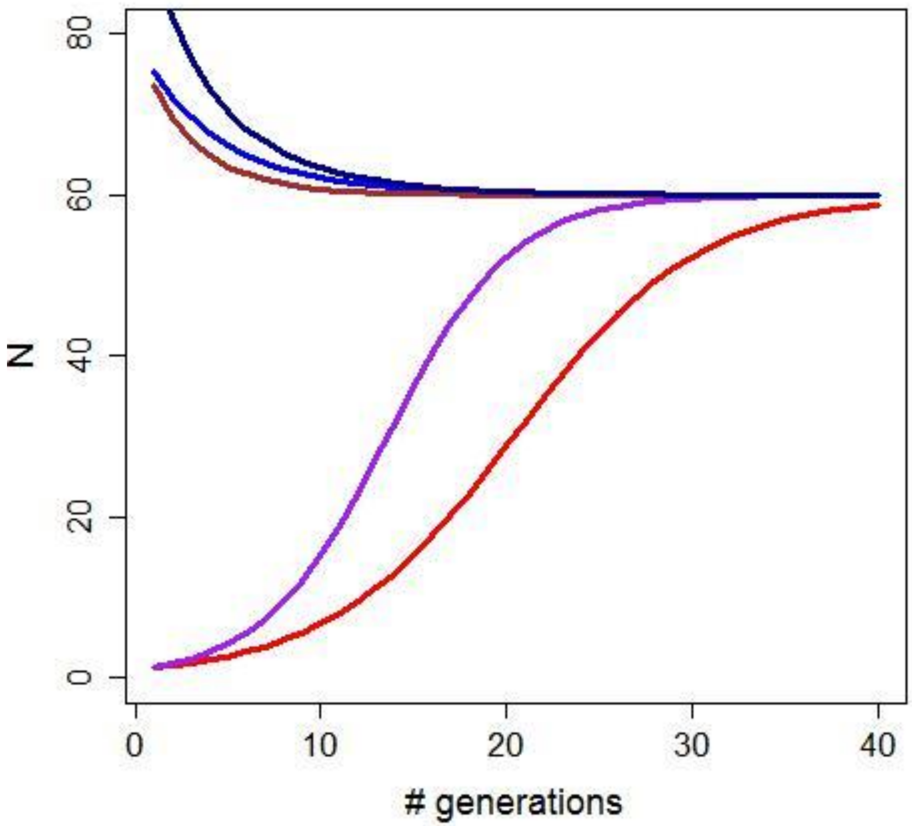
r = 0.2, N_0 = 80

r = 0.3, N_0 = 1

r = 0.2, N_0 = 1

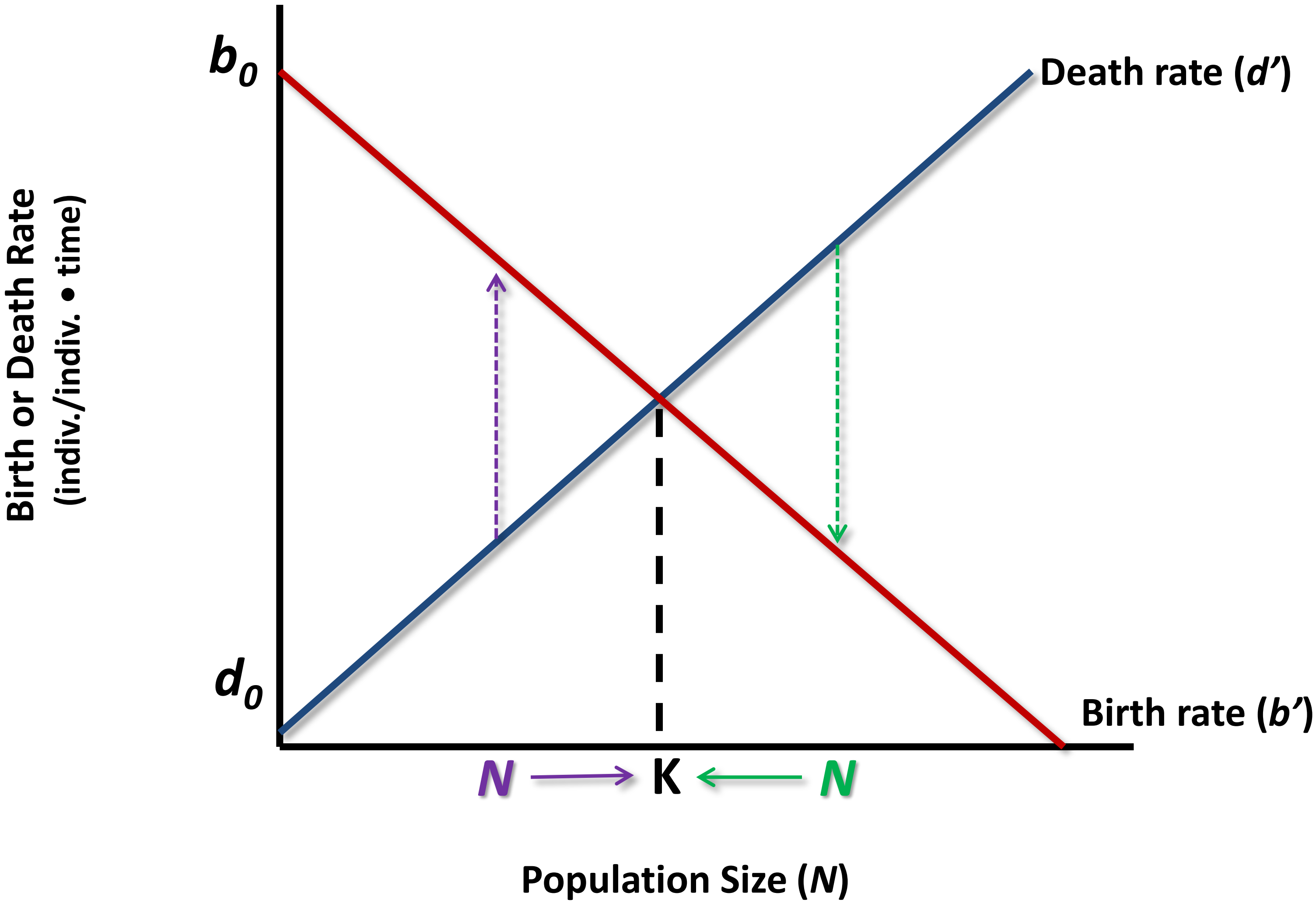
$$N_t = \frac{K}{1 + [(K - N_0)/N_0]e^{-rt}}$$

Logistic population growth



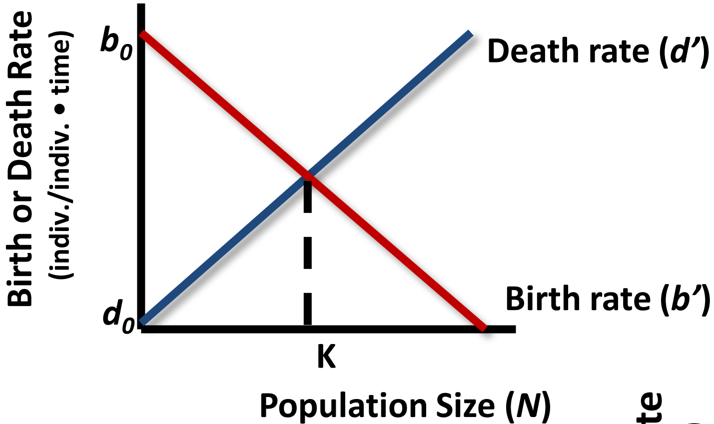
Why would a population ever exceed K?

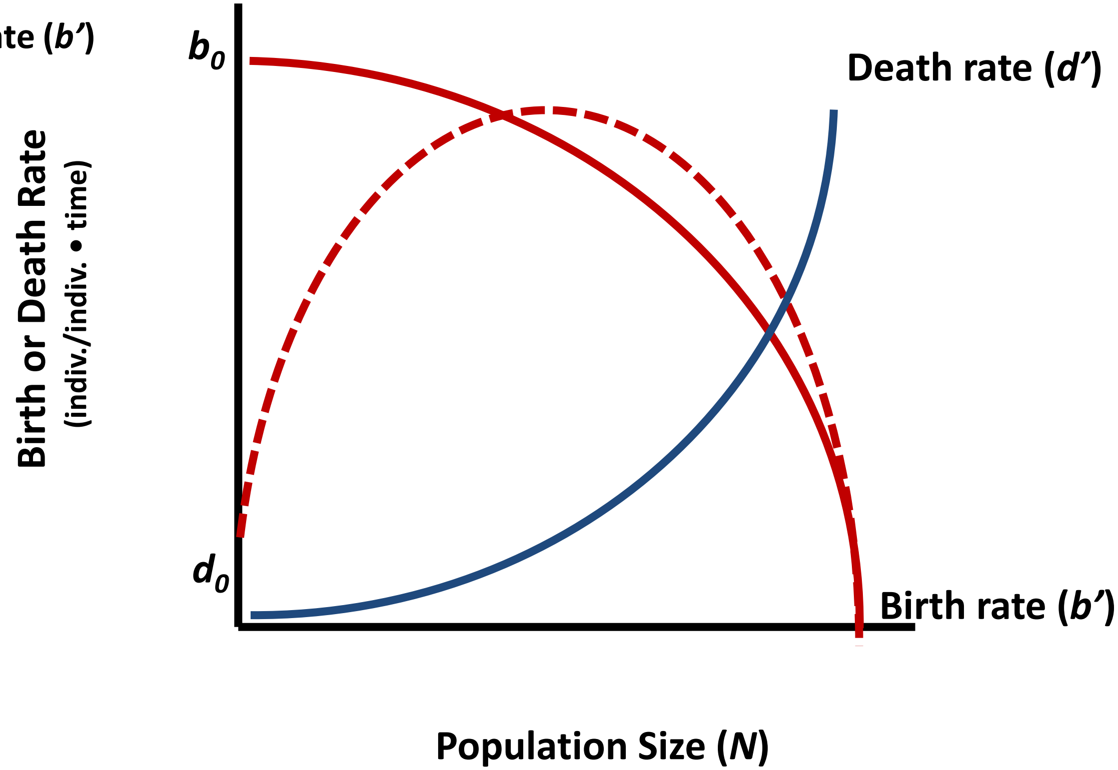
K is an Equilibrium Point



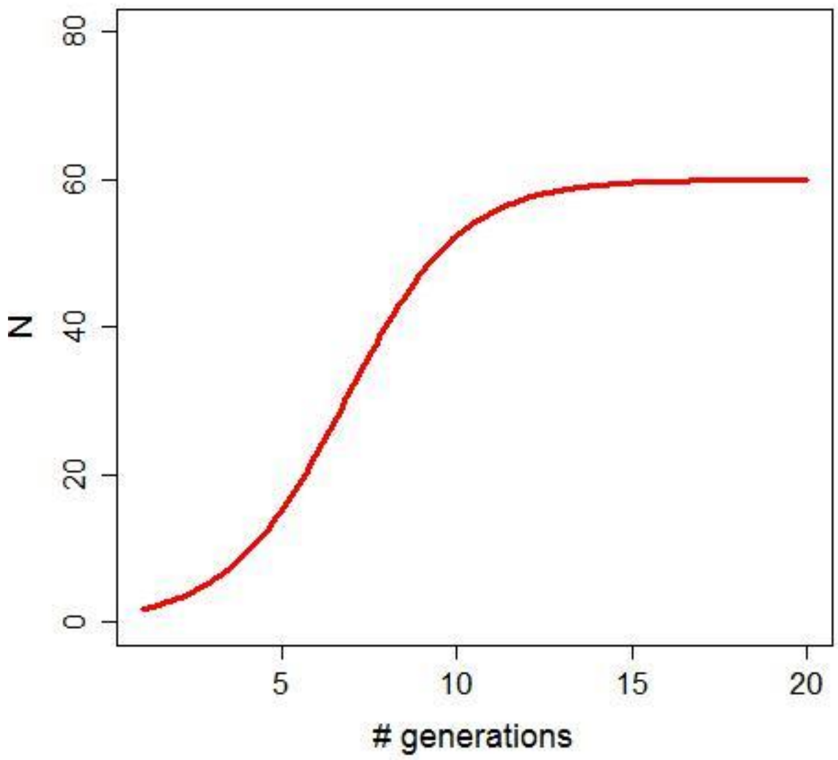
What does K represent biologically?

Assumption of Linear density-dependence





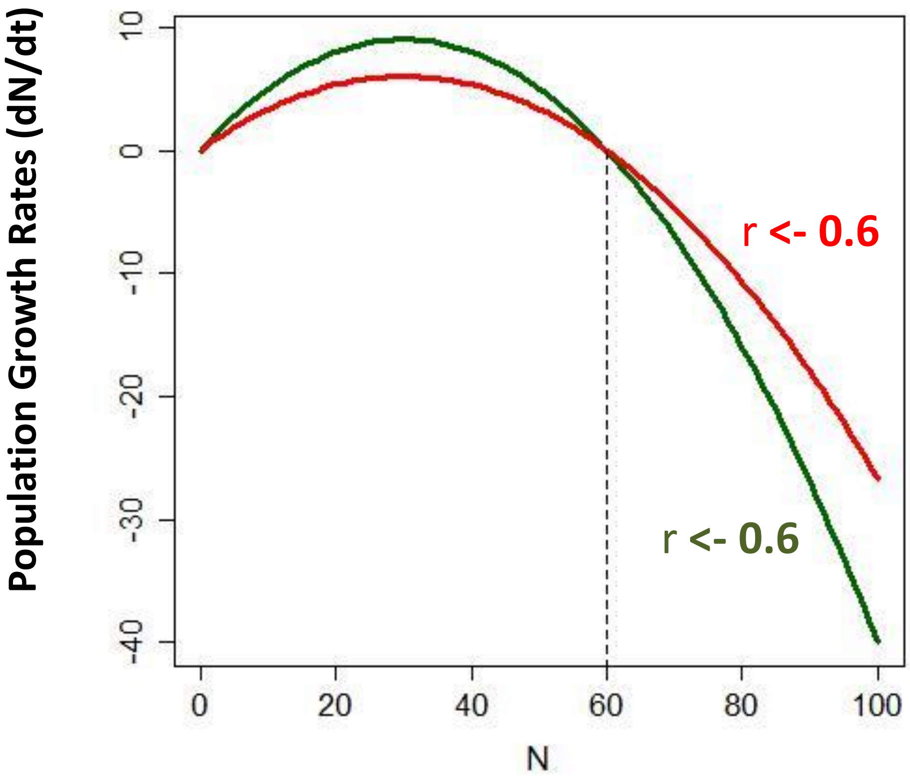
Logistic population growth




```
N <- seq(0,100,1)
t <- seq(1,20,0.1)
N0 <- 1
K <- 60
r <- 0.6

Nt <- K/(1+((K-N0)/N0)*exp(-r*t))
```

At what point is the population growing fastest?

Population growth rate




```
N <- seq(0,100,1)
N0 <- 1
K <- 60
r <- 0.6
r1 <- 0.4

dndt <- r*(1-(1/K)*N)*N
dndt1 <- r1*(1-(1/K)*N)*N
```

Model Assumptions

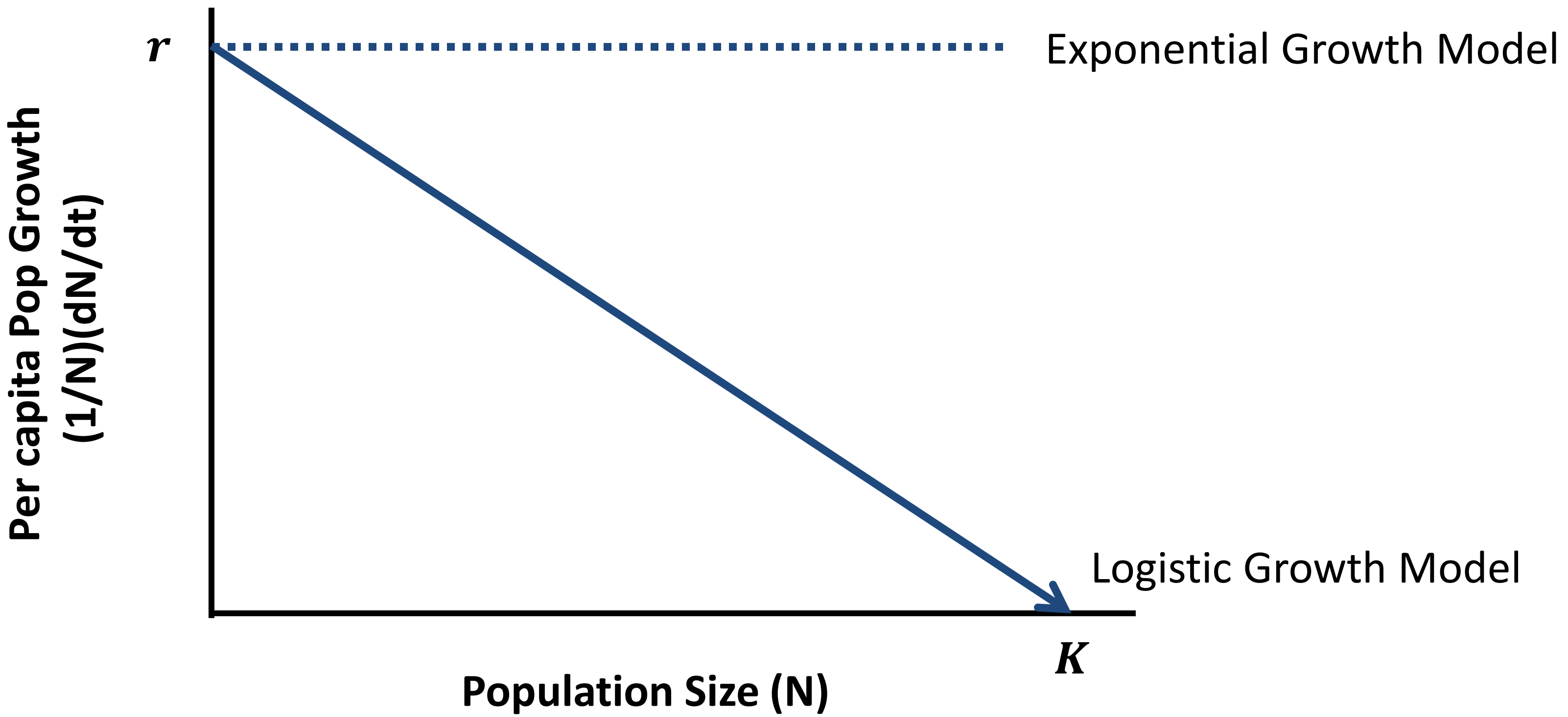
- **Same Assumptions as Exponential Model**

1. **No time lags**
2. **No migration**
3. **No Genetic Variation**
4. **No Age Structure**

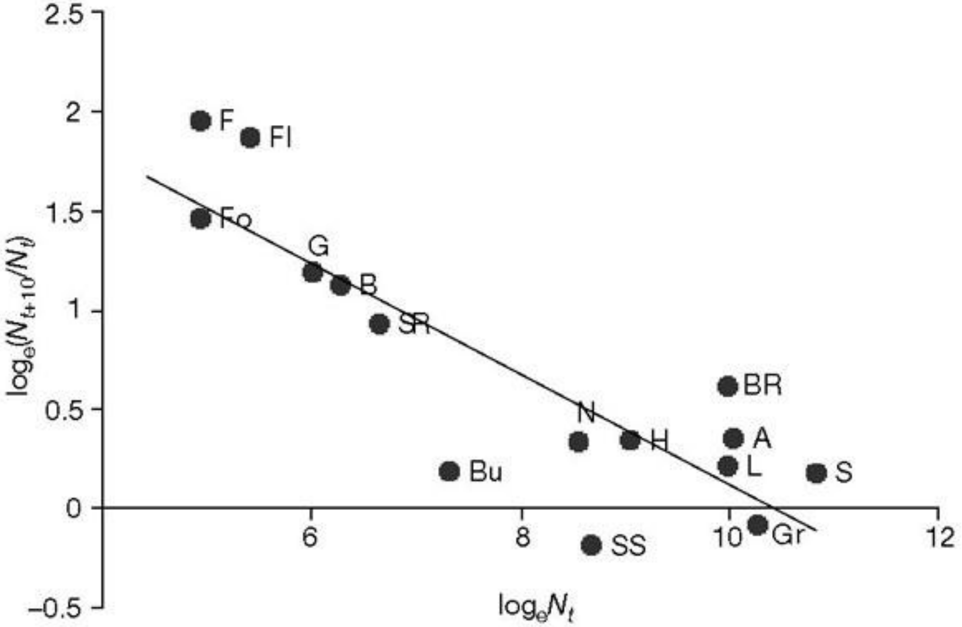
- **Additional 2 Assumptions**

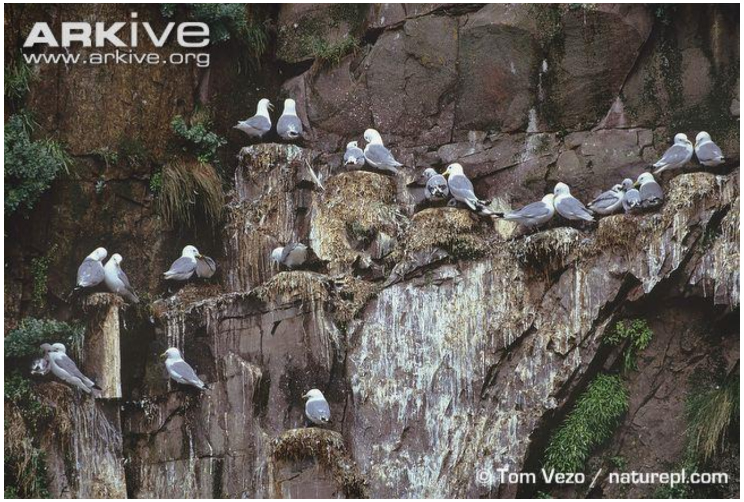
1. **Constant carry capacity** – this means that resource availability does not vary with time and K is constant.
2. **Linear density dependence** – this assumes that each individual added to the population causes an incremental decrease in the **per capita rate of population growth** [(*1/N*)(*dN/dt*)].

Per capita rate of Population Growth



Per capita population growth





[Evidence of intra-specific competition for food in a pelagic seabird]
S. Lewis, T. N. Sherratt, K. C. Hamer and S. Wanless
Nature 412, 816-819(23 August 2001)
doi:10.1038/35090566

Time Lags

- **In a continuously growing population, adding new individuals into the population causes a continuous decrease in the per capita rate of population growth [($1/N$)(dN/dt)]**

- **However, in many populations there are <u>time lags</u> (τ) in response to changes in population size**

What could cause these time lags?

Time Lags

- **The change in population size at time *t* is now controlled by the population size at some point (t-τ) in the past ($N_{t-\tau}$)**

- **build this into a delay differential equation into the logistic model as:**
- $\frac{dN}{dt} = rN\left(1 - \frac{N_{t-\tau}}{K}\right)$

- **Two things will affect this equation.**

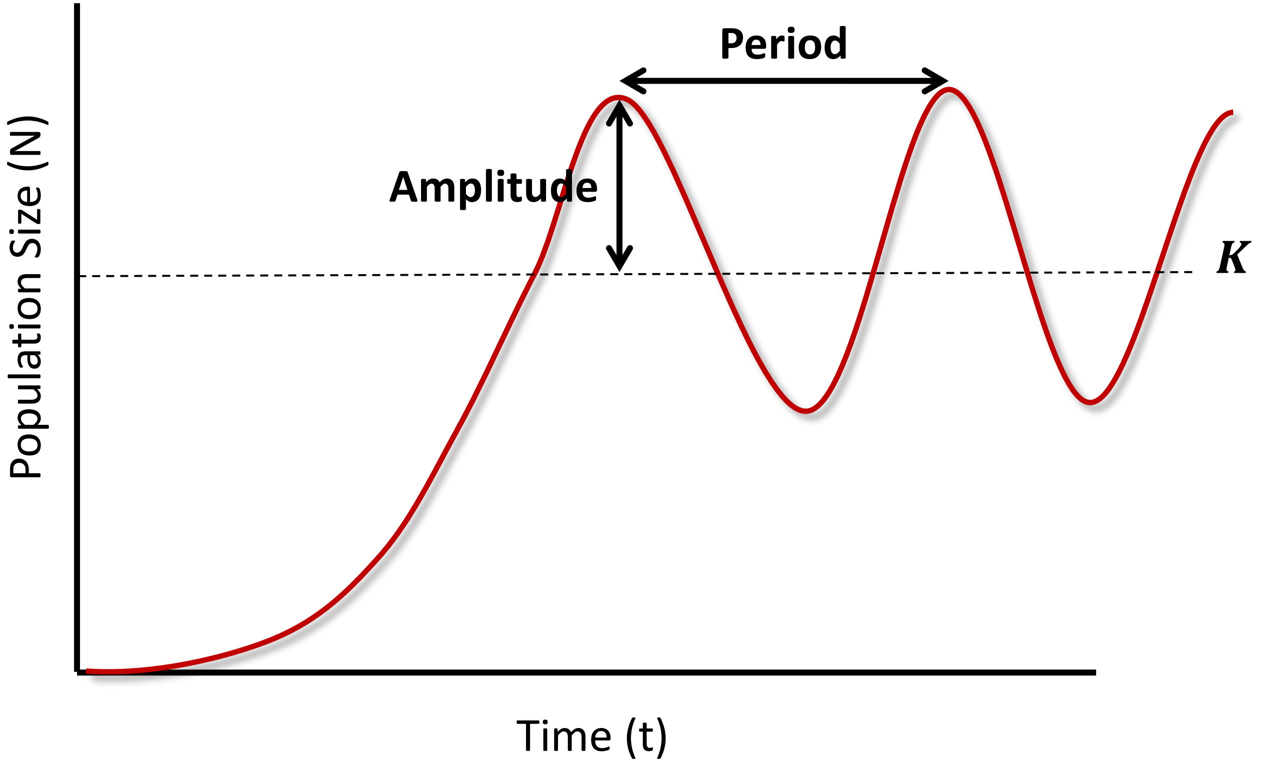
1. **The length of the time lag (τ)**
2. **The response time of the population – this is inversely related to the intrinsic rate of increase (i.e. 1/r).**

Time Lags

- **The ratio of the time lag to the response time $\frac{\tau}{1/r}$, (which is simply $r\tau$) controls population growth.**

- **If $r\tau$ is small** (between 0 to 0.368)
  - the population increases smoothly to a carrying capacity
- **If $r\tau$ is moderate** (0.368 to 1.570)
  - the population first overshoots then undershoots carrying capacity, followed by dampening oscillation to reach carrying capacity over time.
- **If $r\tau$ is large** (>1.570)
  - the population goes into a stable limit cycle of oscillations above and below carrying capacity that go on indefinitely.

Cyclic Populations



Time Lags

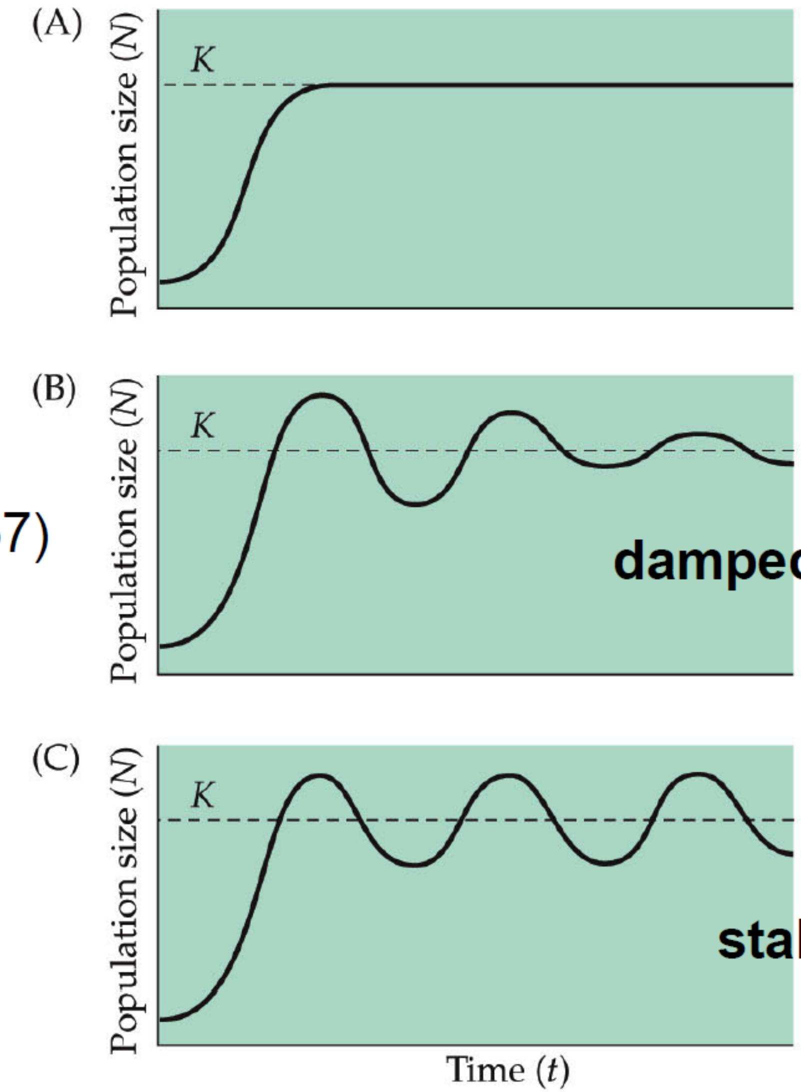
$$\frac{dN}{dt} = rN\left(1 - \frac{N_{t-\tau}}{K}\right)$$

$$\frac{\tau}{1/r}, = r\tau$$

($0 < r\tau < 0.368$),

($0.368 < r\tau < 1.57$)

($r\tau > 1.57$)

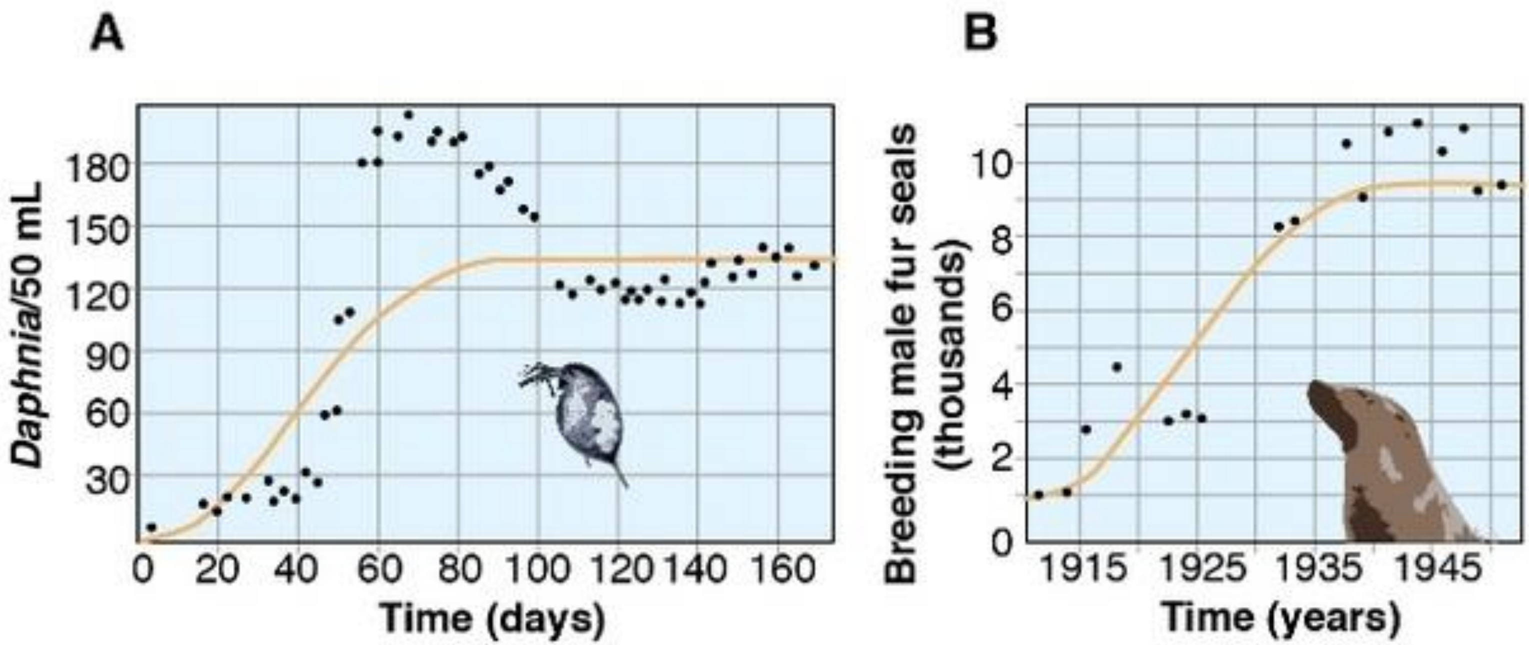


damped oscillations

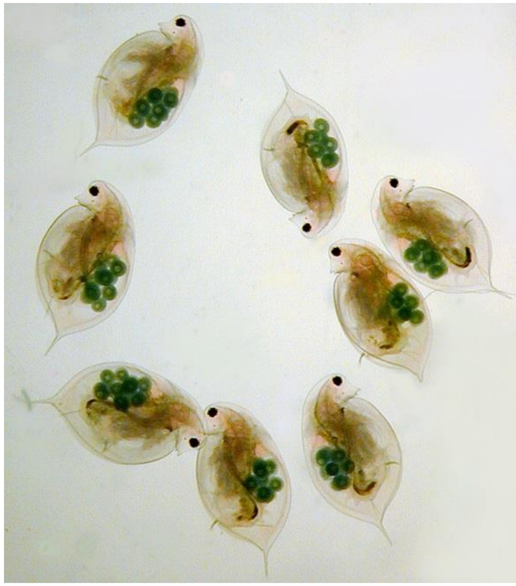
stable limit cycle

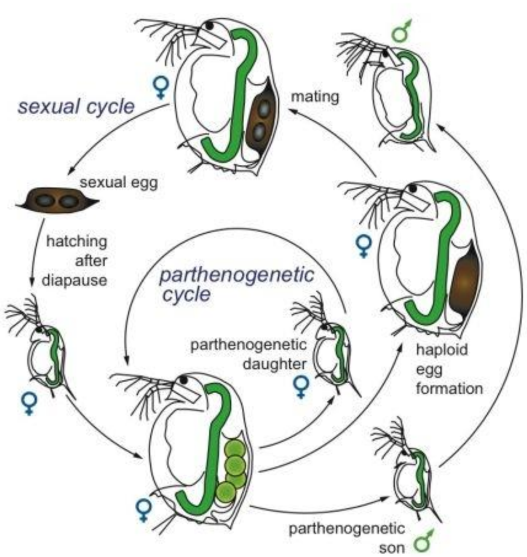
***ECOLOGY*, Figure 10.9**

Logistic population growth

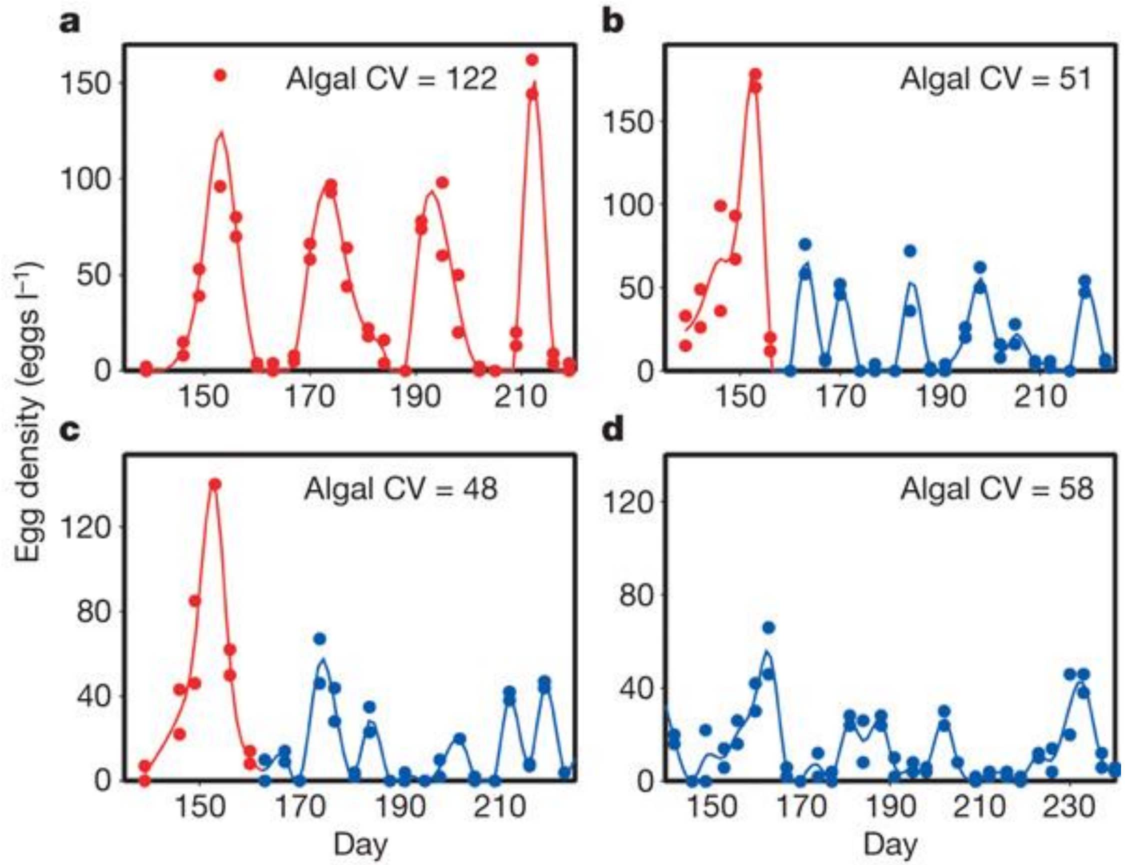


Daphnia pulex





Egg density dynamics during cycles.



E McCauley *et al. Nature* **455**, 1240-1243 (2008) doi:10.1038/nature07220