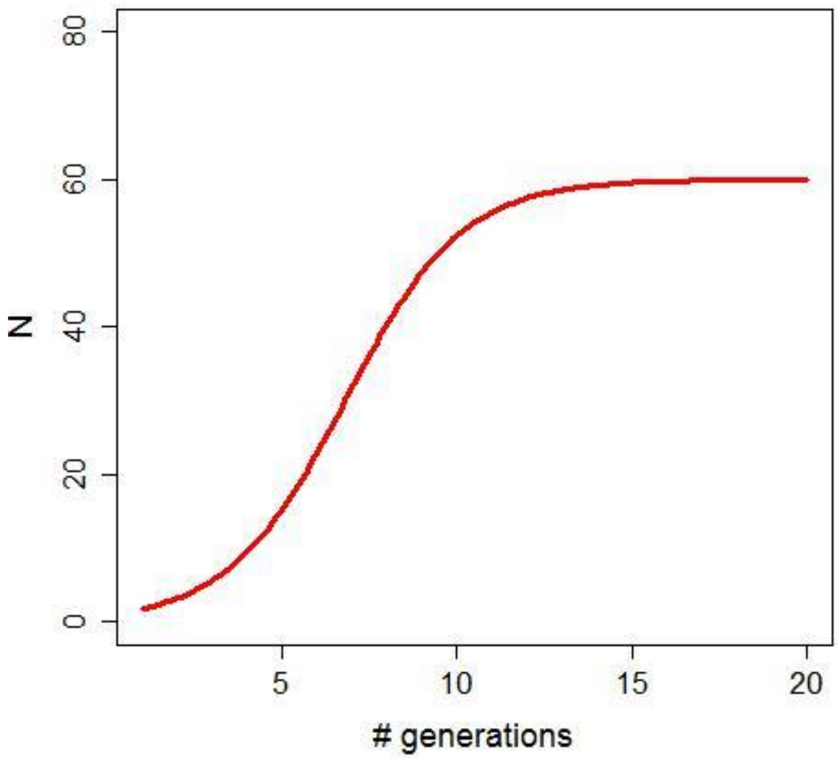
BIOL 410 Population and Community Ecology

Density-dependent growth 2

Objectives

- Time lags
- Amplitude, period
- Equilibrium
- Damped oscillations
- Stable limit cycles
- Discrete logistic growth model
- Chaos vs. stochasticity

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))
```

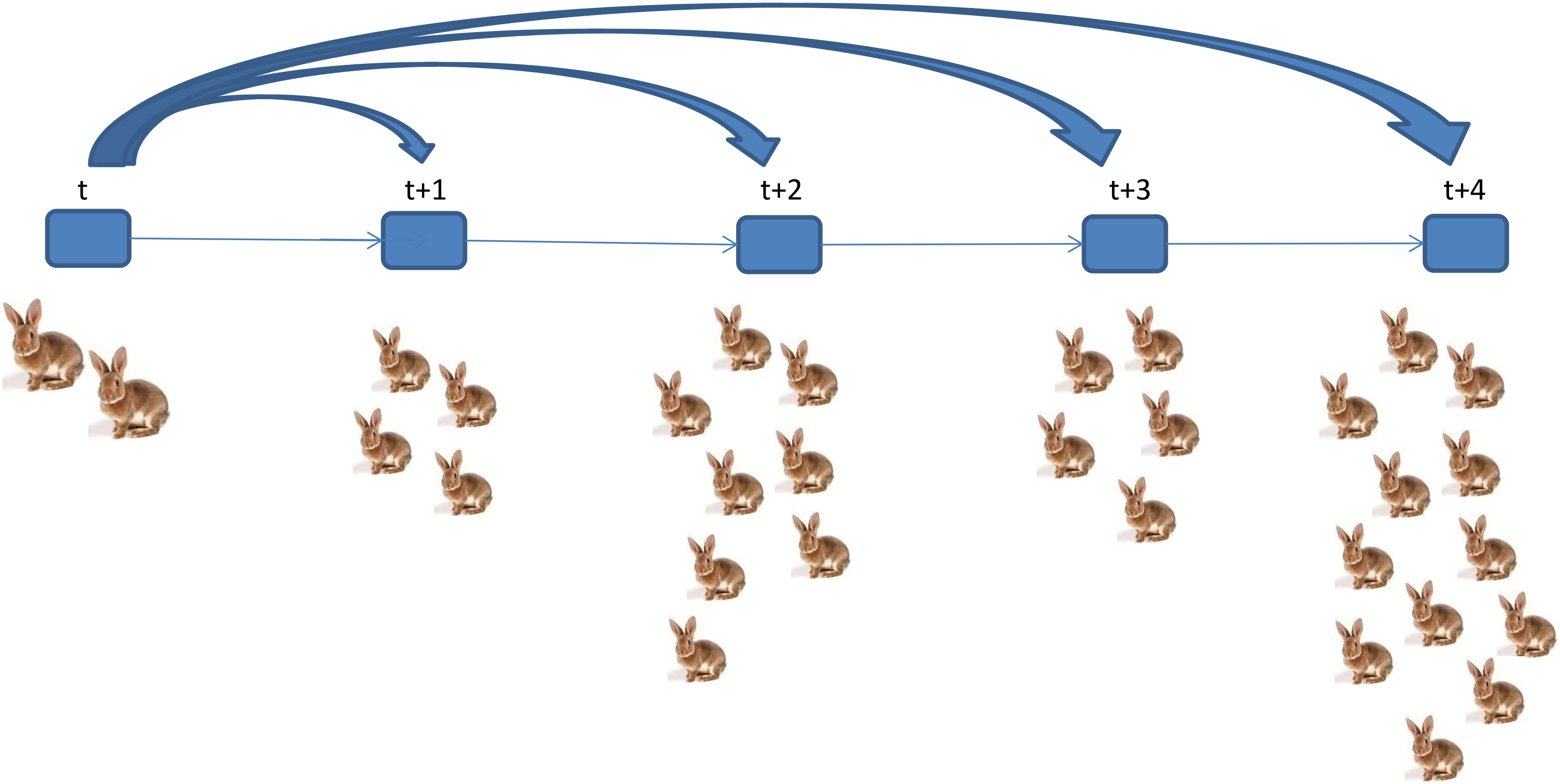
Time Lags

- **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 time lags (τ) in response to changes in population size**

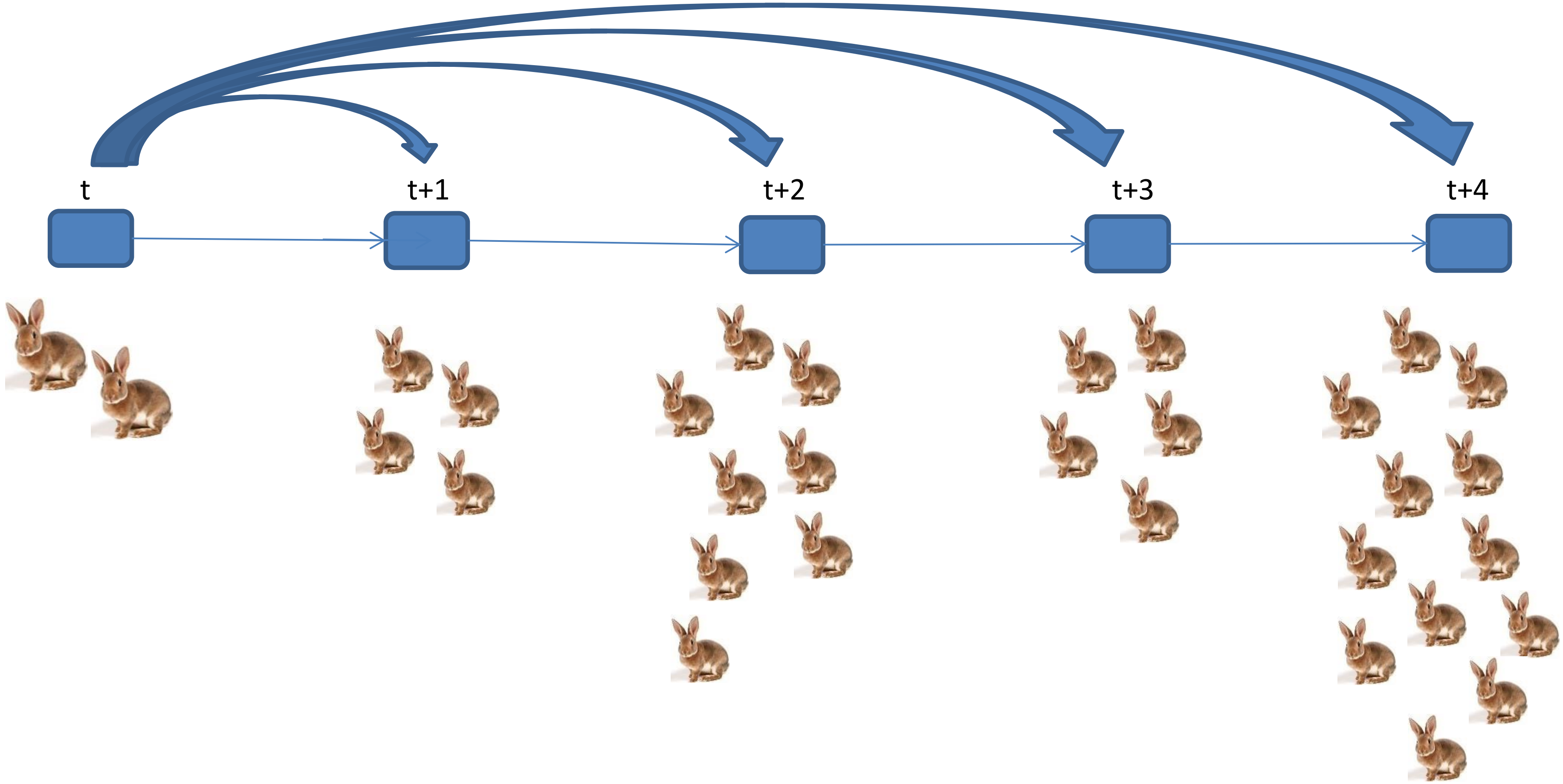
What could cause these time lags?

Time Lags



What could produce time lags in density dependence?

Time Lags



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

τ = time lag

Time Lags

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

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

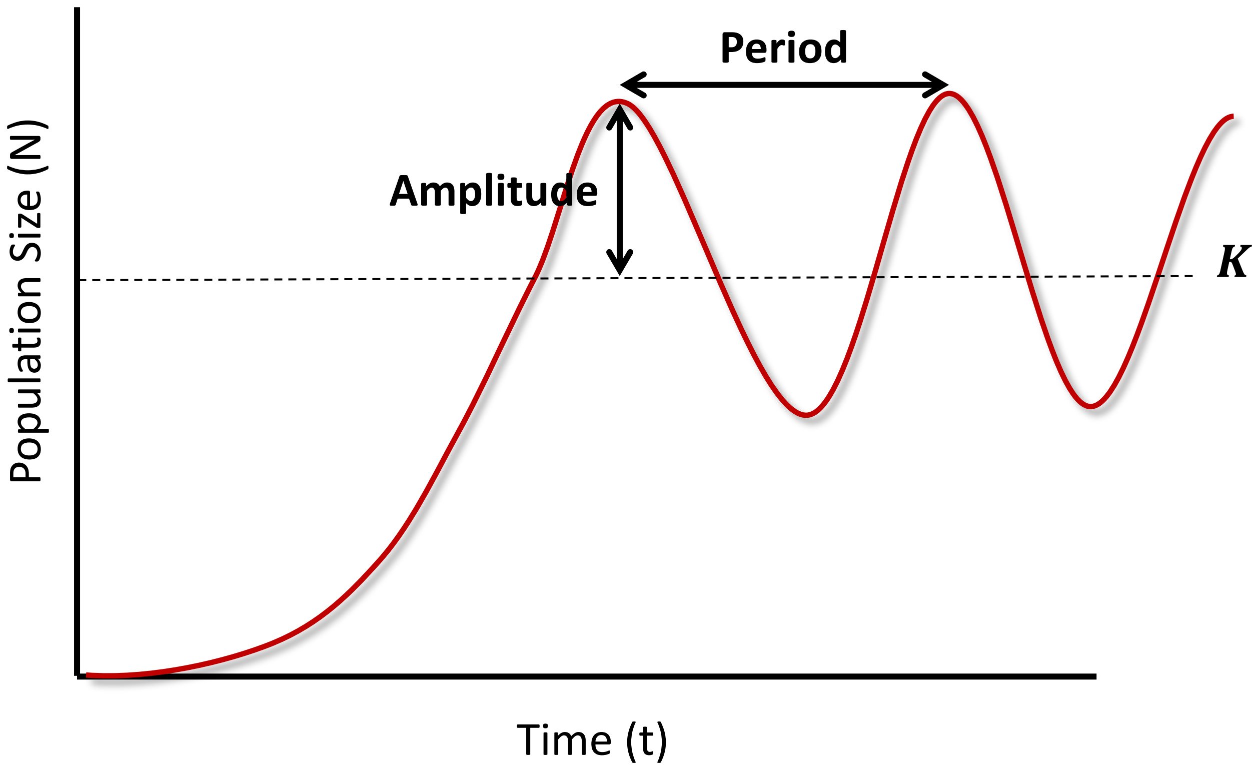
1. **The length of the time lag (*τ*)**
2. **The response time of the population – this is inversely related to the intrinsic rate of increase (i.e. 1/*r*).**

Time Lags

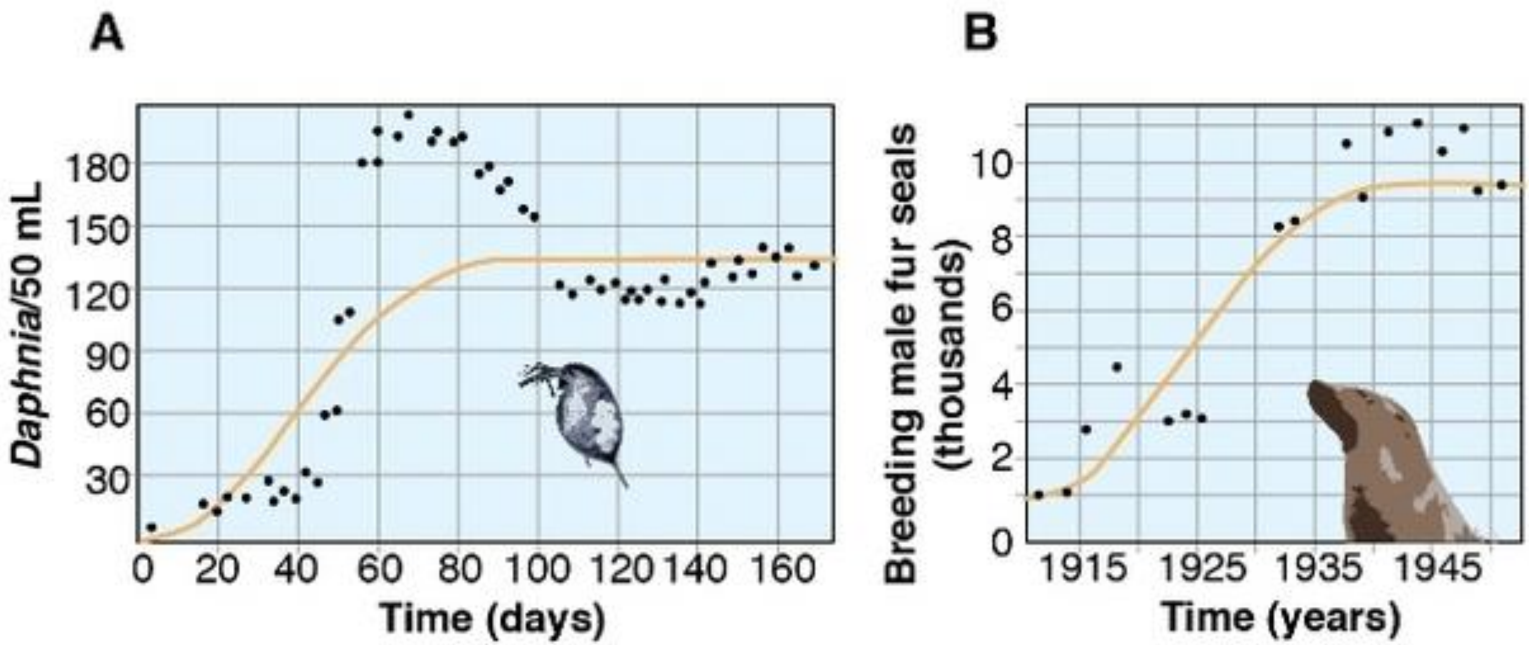
- **The ratio of the time lag to the response time $\frac{\tau}{1/r}$, (which is simply $r\tau$) controls population growth.**

- **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.

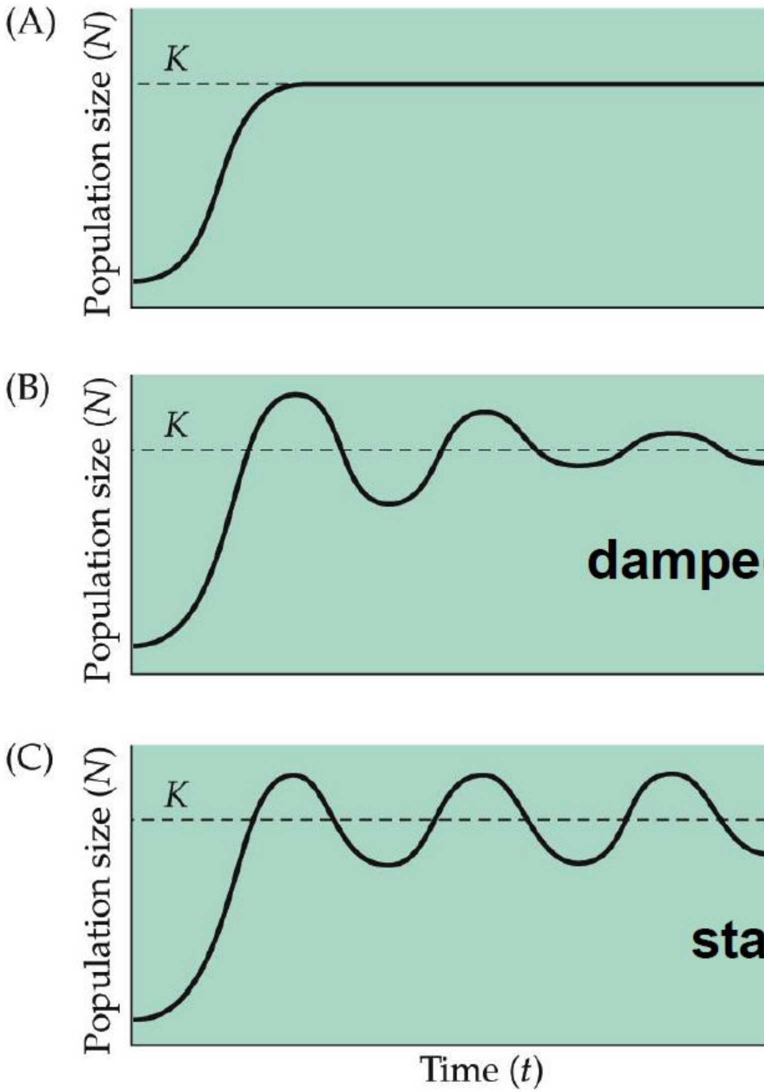
Cyclic Populations



Logistic population growth



Time Lags



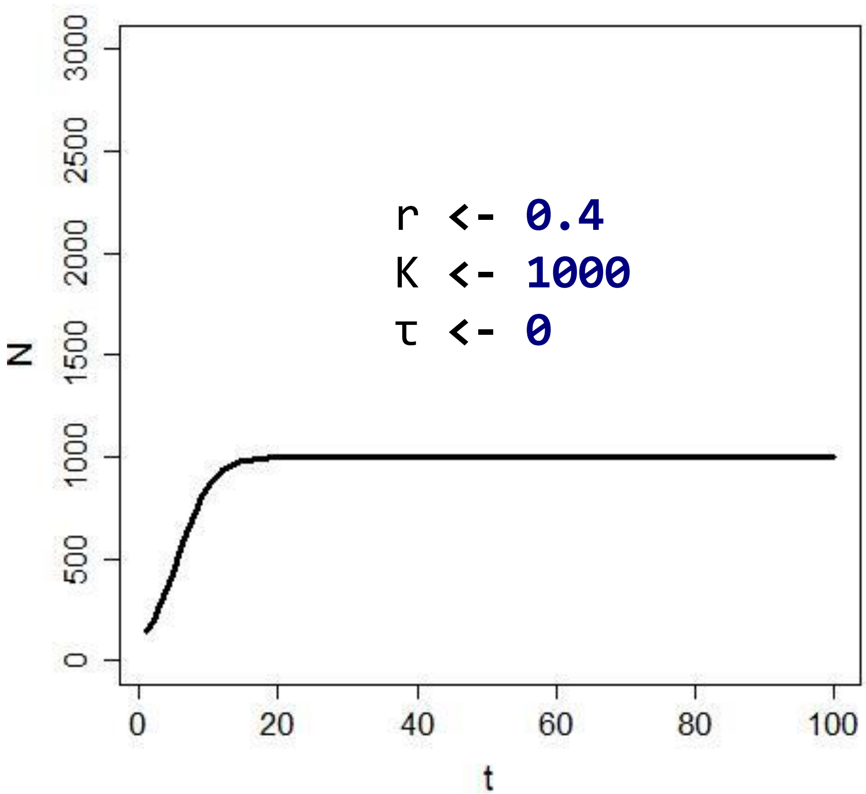
damped oscillations

stable limit cycle

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

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

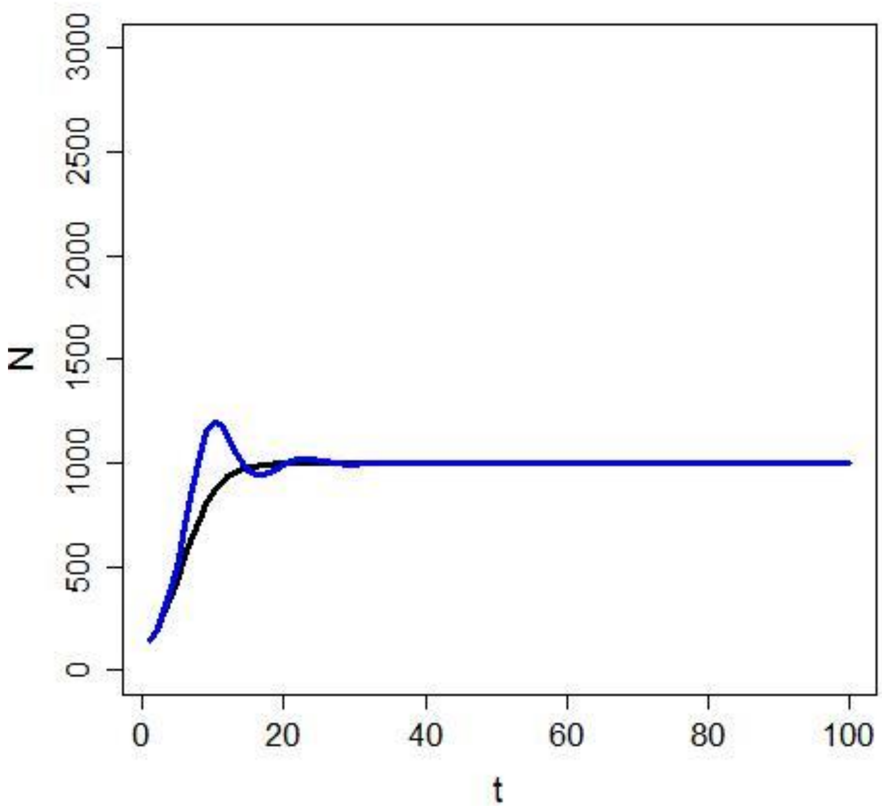
Time lags (continuous population)



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

```
t <- seq(1,100,1)
N0 <- 100
r <- 0.4
K <- 1000
tau <- 0
rtau <- r*tau
N <- seq(0,length(t),1)
N[1]<-N0
lambda <- exp(r)
for(ts in t){
etau <- tau
if(ts <= tau) etau <- 0
  N[ts+1] <- lambda*N[ts]/(1+((N[ts-
  etau]*(lambda-1))/K))
}
```

Time lags (continuous population)



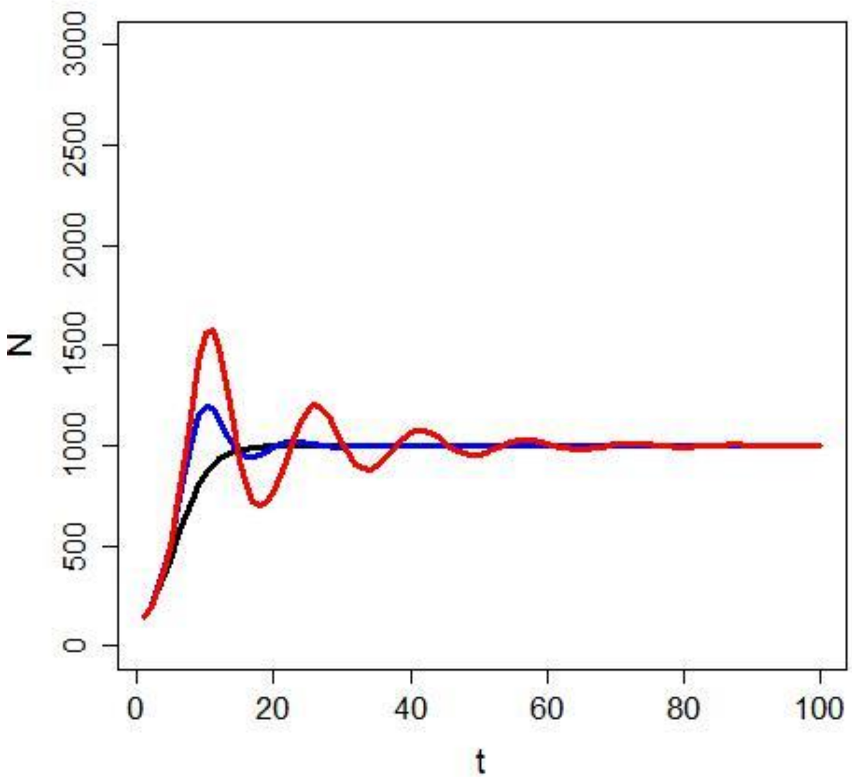
$$\frac{dN}{dt} = rN\left(1 - \frac{N_{t-\tau}}{K}\right)$$

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

0 < rτ < 0.368 < rτ < 1.57

```
r <- 0.4
K <- 1000

τ <- 0, rτ = 0
τ <- 2, rτ = 0.8
```

Time lags (continuous population)



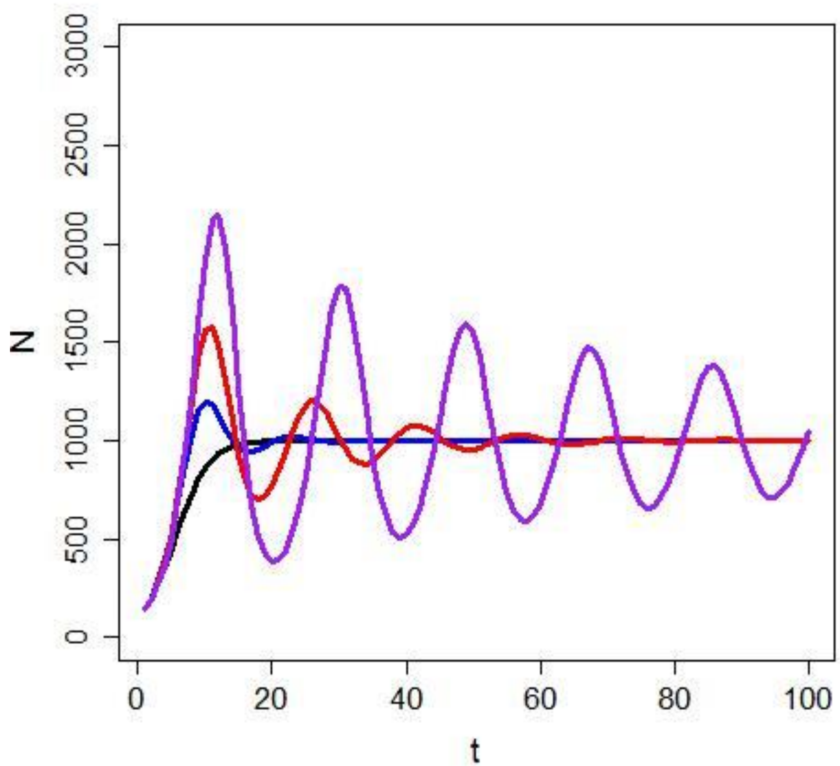
$$\frac{dN}{dt} = rN\left(1 - \frac{N_{t-\tau}}{K}\right)$$

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

0 < rτ < 0.368 < rτ < 1.57

```
r <- 0.4
K <- 1000

τ <- 0, rτ = 0
τ <- 2, rτ = 0.8
τ <- 3, rτ = 1.2
```

Time lags (continuous population)



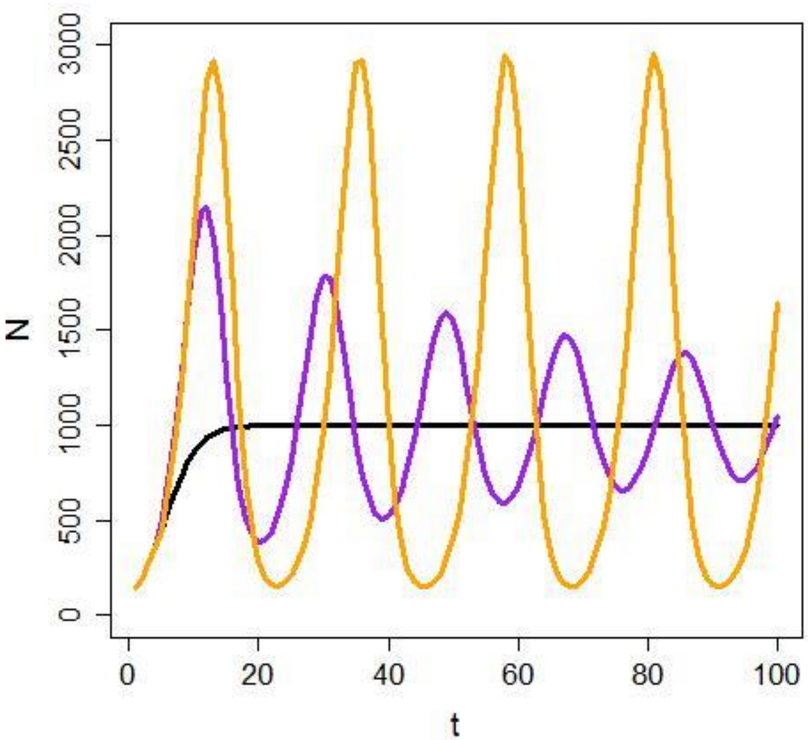
$$\frac{dN}{dt} = rN\left(1 - \frac{N_{t-\tau}}{K}\right)$$

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

$0 < r\tau < 0.368 < r\tau < 1.57$

```
r <- 0.4
K <- 1000

τ <- 0, rτ = 0
τ <- 2, rτ = 0.8
τ <- 3, rτ = 1.2
τ <- 4, rτ = 1.6
```

Time lags (continuous population)



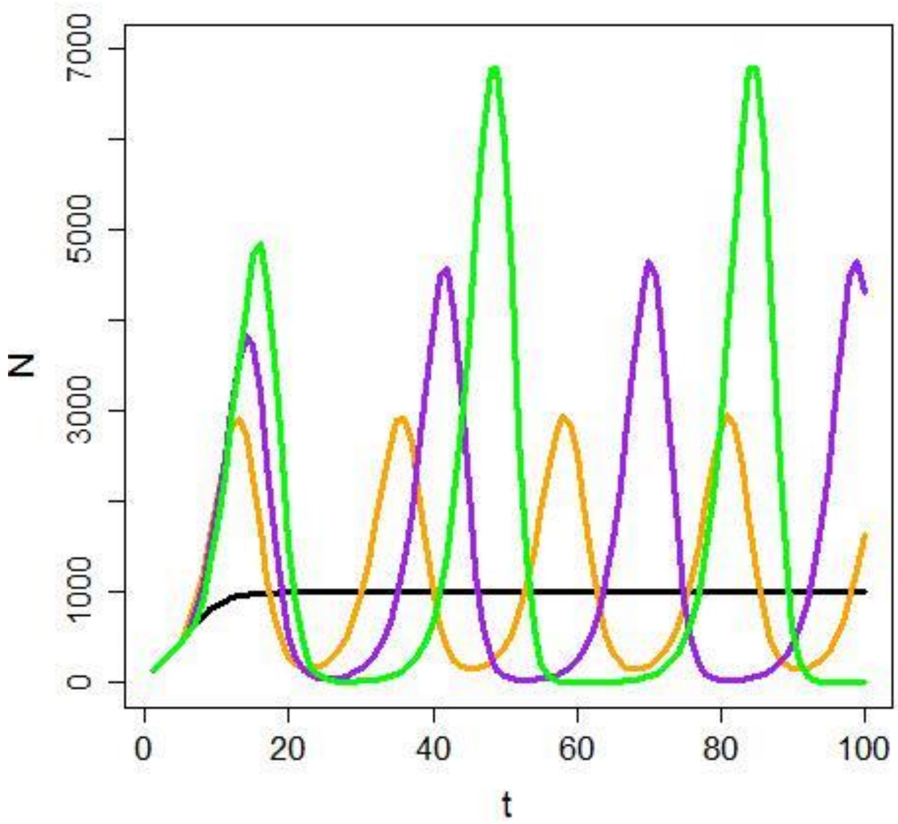
$$\frac{dN}{dt} = rN\left(1 - \frac{N_{t-\tau}}{K}\right)$$

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

$0 < r\tau < 0.368 < r\tau < 1.57$

```
r <- 0.4
K <- 1000

τ <- 0, rτ = 0
τ <- 4, rτ = 1.6
τ <- 5, rτ = 2.0
```

Time lags (continuous population)



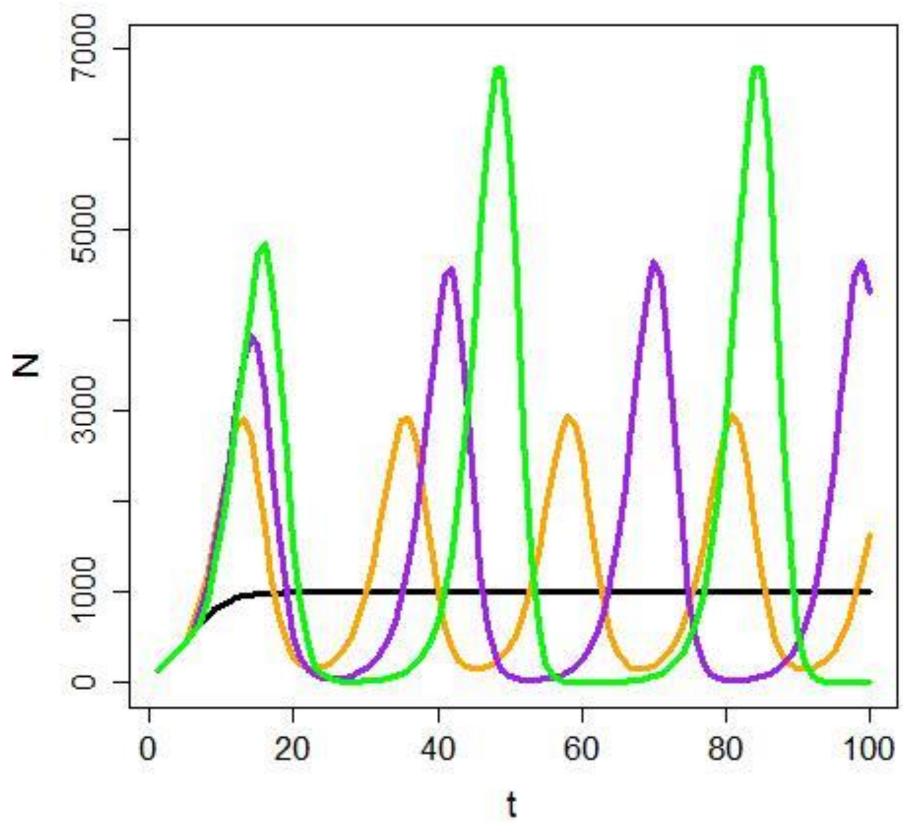
$$\frac{dN}{dt} = rN\left(1 - \frac{N_{t-\tau}}{K}\right)$$

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

0.368 < rτ < 1.57 < rτ

```
r <- 0.4
K <- 1000

τ <- 0, rτ = 0
τ <- 5, rτ = 2.0
τ <- 6, rτ = 2.4
τ <- 7, rτ = 2.8
```

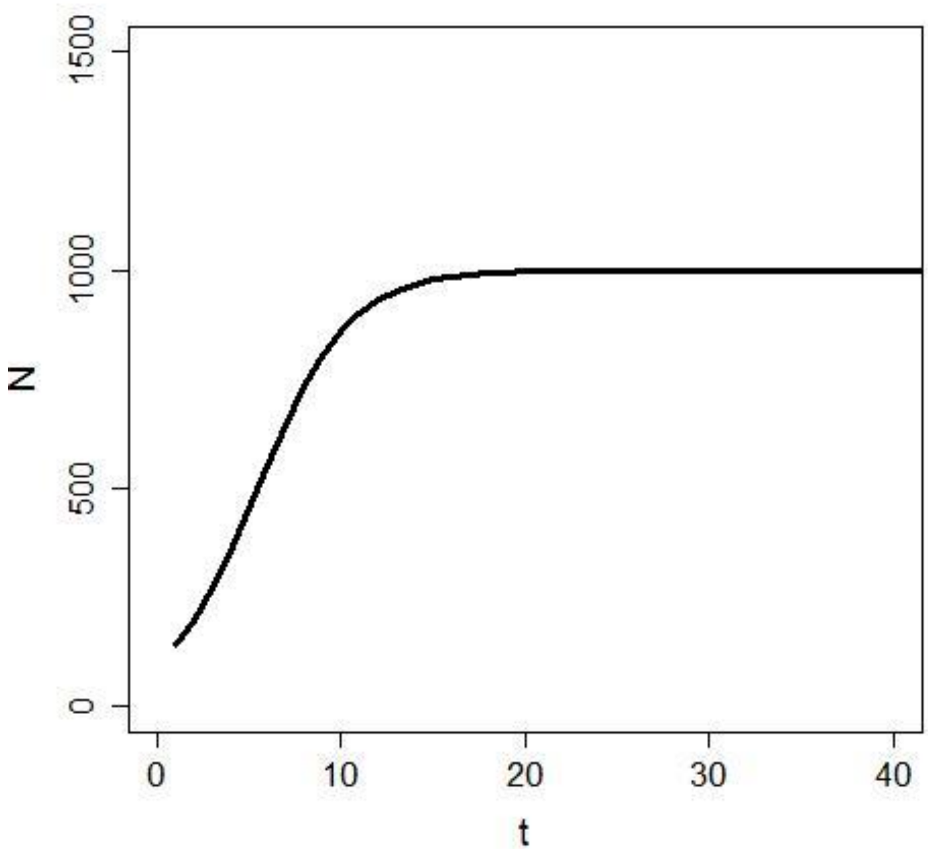
Time lags (continuous population)



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

- What will happen if these populations exhibiting limit cycles are disturbed?
- Land slip, fire?

Time lags (continuous population)

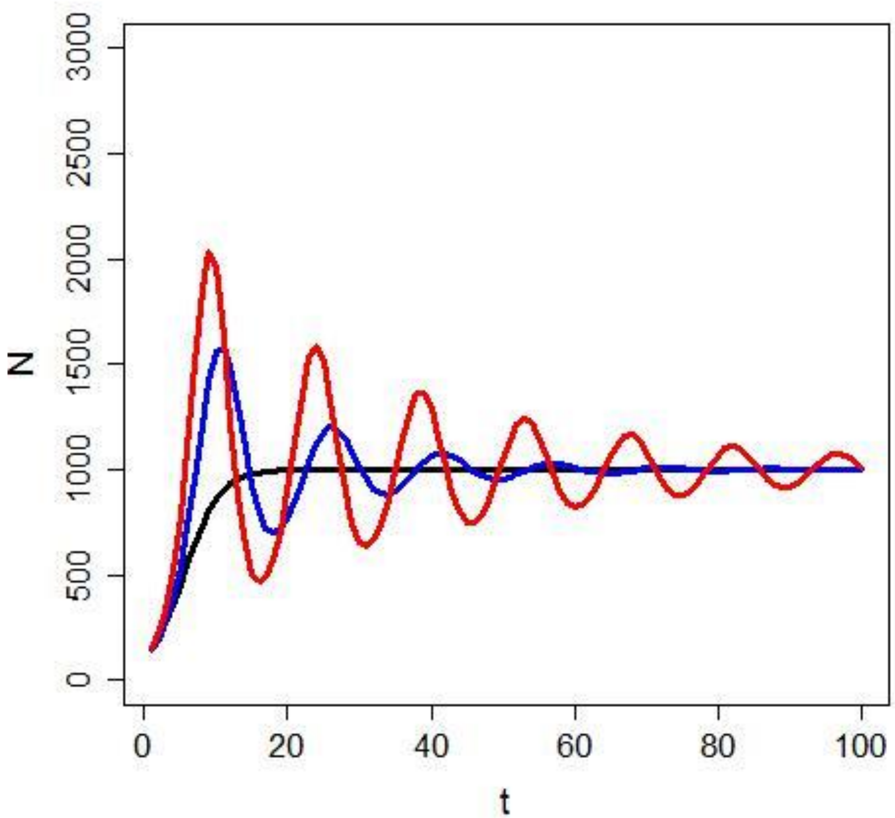


$$\frac{dN}{dt} = rN\left(1 - \frac{N_{t-\tau}}{K}\right)$$

```
r <- 0.4
K <- 1000

τ <- 0, rτ = 0
```

What is the impact of τ <- 0?

Time lags (continuous population)



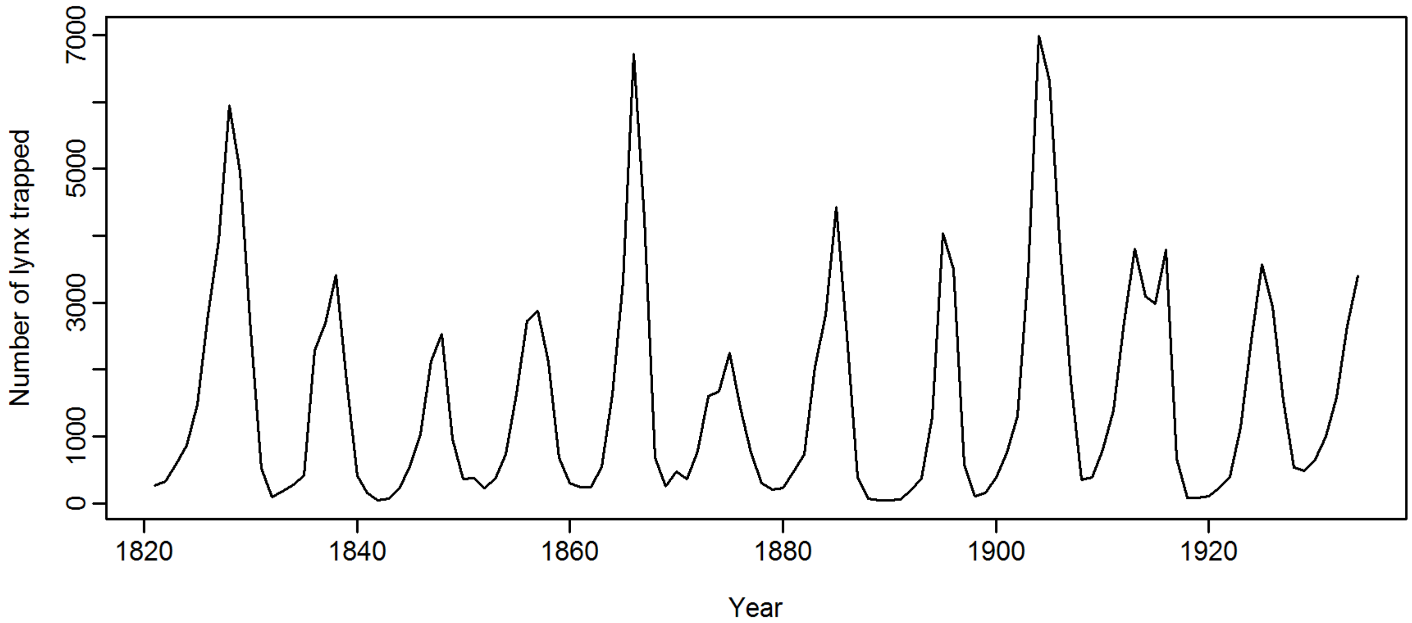
$$\frac{dN}{dt} = rN\left(1 - \frac{N_{t-\tau}}{K}\right)$$

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

0.368 < rτ < 1.57 < rτ

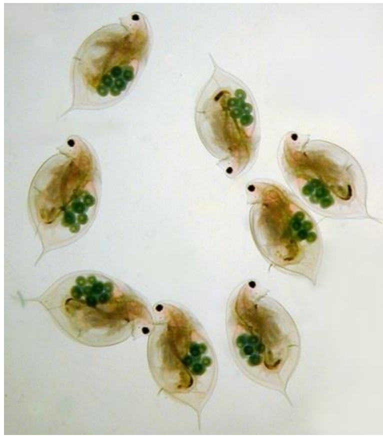
```
K <- 1000

τ <- 0, r <- 0.4, rτ = 0
τ <- 3, r <- 0.4, rτ = 1.2
τ <- 3, r <- 0.5, rτ = 1.5
```

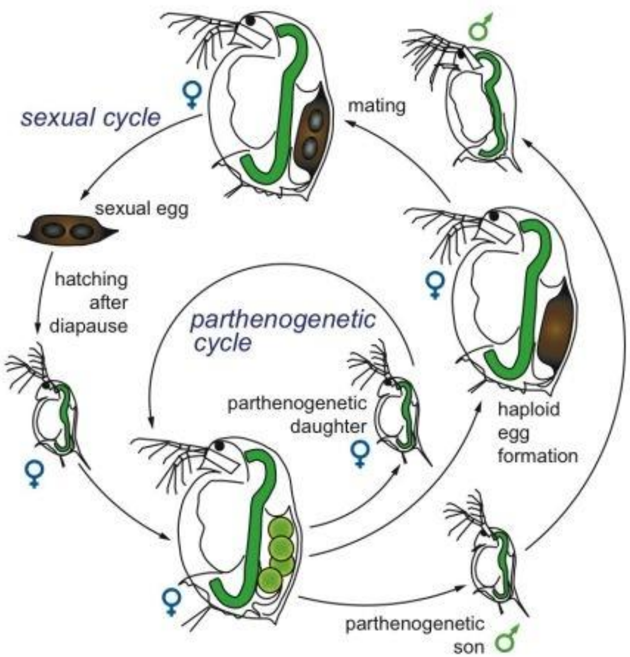
Cycles in ecological populations



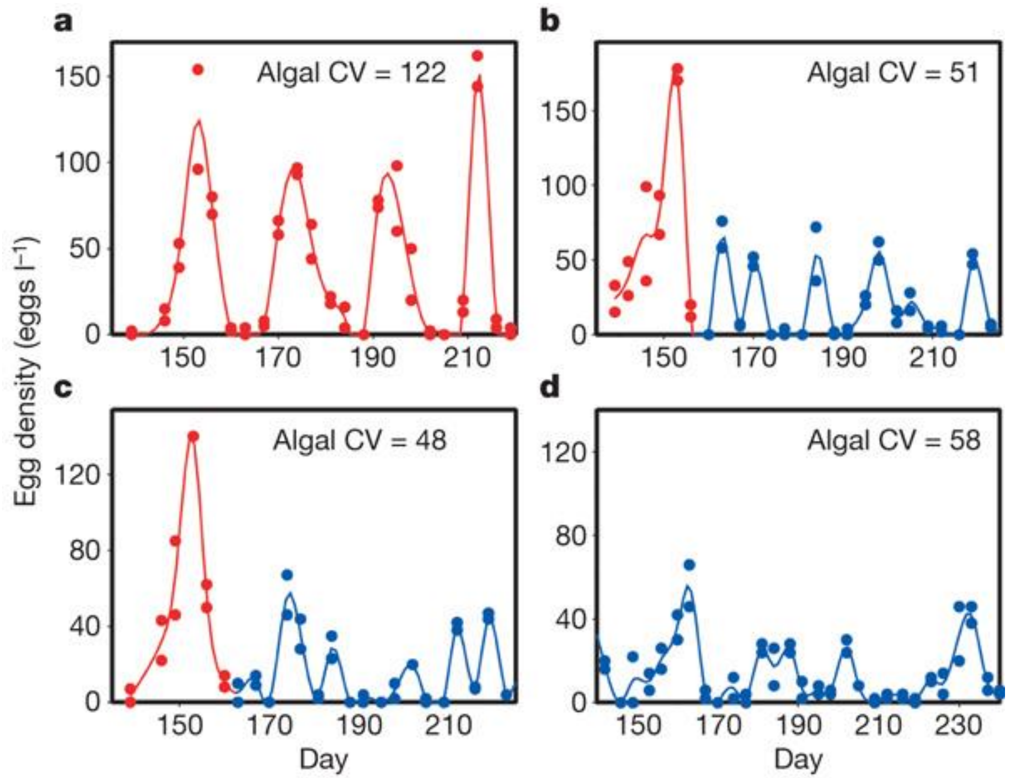
Canadian lynx data — the number of lynx trapped each year in the McKenzie river district of northwest Canada (1821–1934).

Daphnia pulex



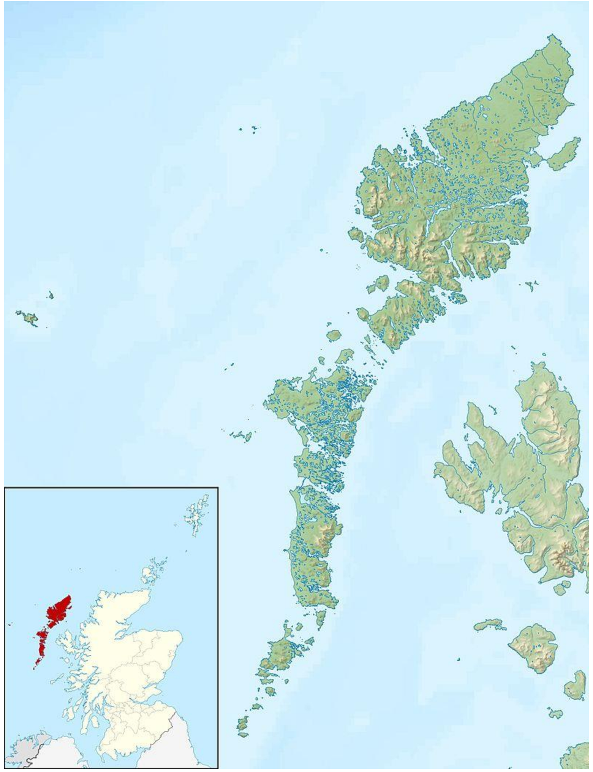


Egg density dynamics during cycles.

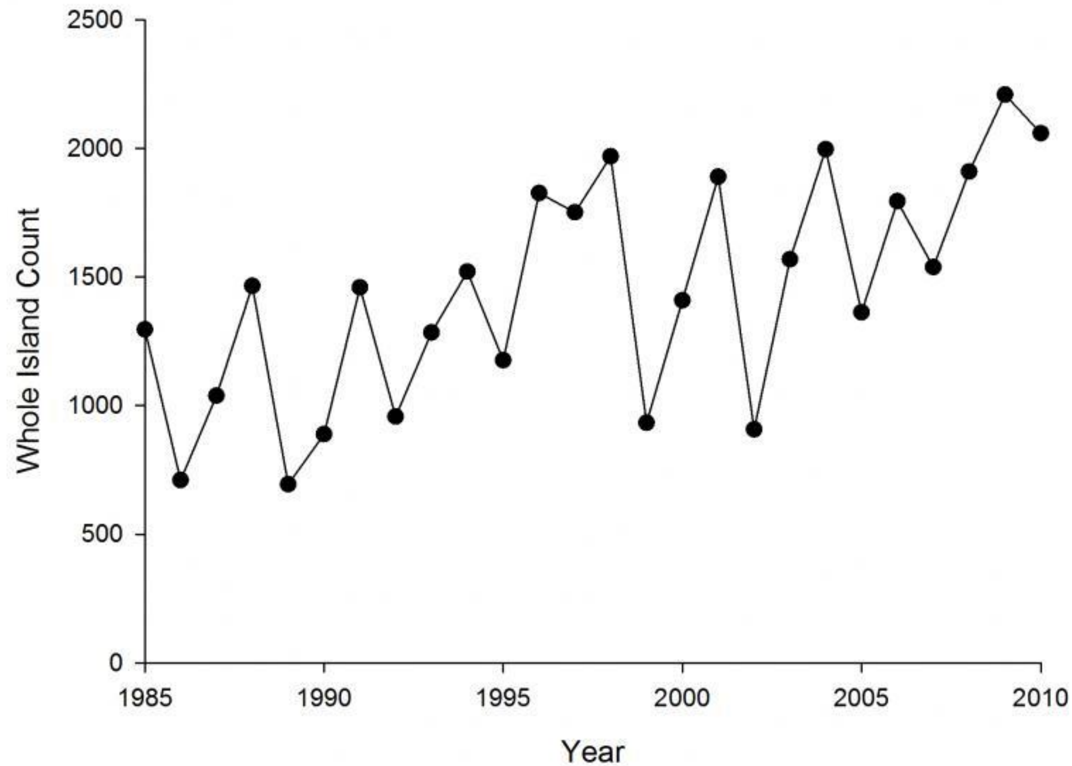


E McCauley *et al. Nature* **455**, 1240-1243 (2008) doi:10.1038/nature07220

St Kilda, Scotland
Soay Sheep

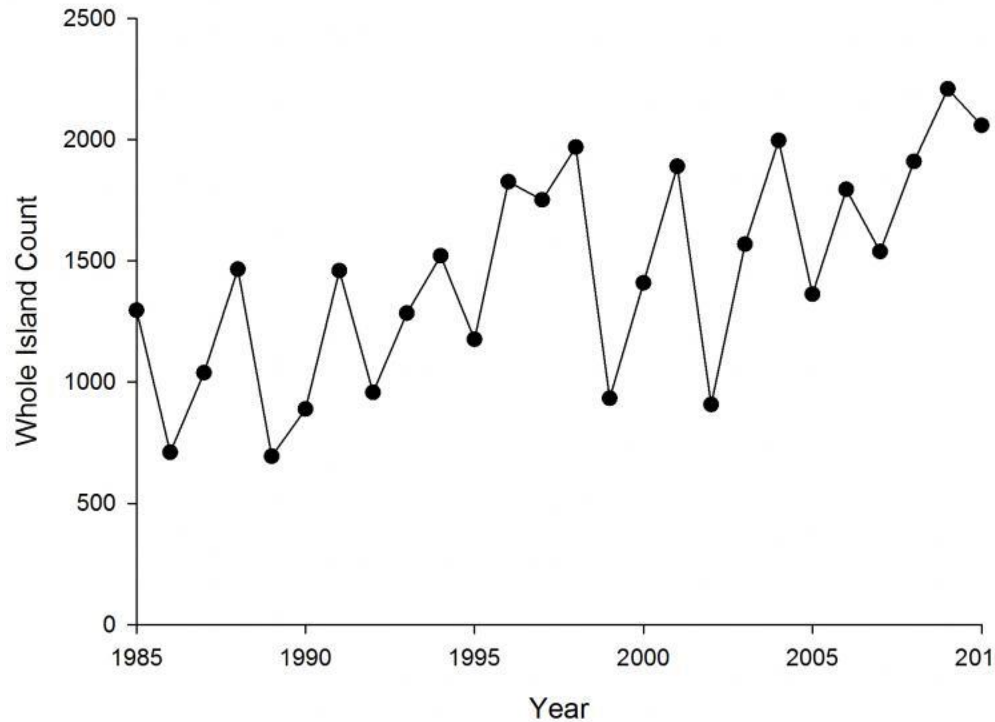


http://soaysheep.biology.ed.ac.uk/



- Approximately 3 years between population crashes
- What drives this cycle?

Grenfell, B. T., O. F. Price, S. D. Albon, and T. H. Clutton-Brock. 1992. Overcompensation and population-cycles in an ungulate. Nature 355:823-826.



- Grenfell et al. 1992
  - Competition for food, highly overcompensating density-dependent mortality
- Grenfell et al. 1998
  - Weather and density dependence
- Coulson et al. 2001
  - Population age-strucure, sex-structure, weather, density-dependence
- Ozgul et al.2009
  - Size of sheep (as well as other factors)

http://soaysheep.biology.ed.ac.uk/

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

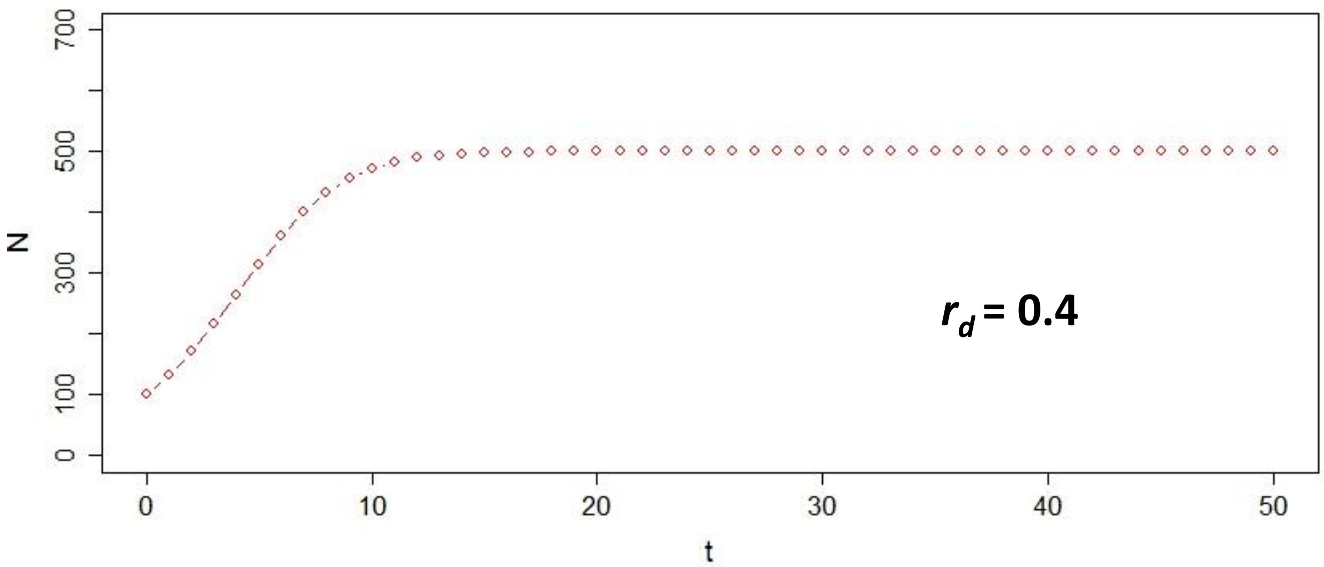
Discrete logistic models

$$N_{t+1} = N_t + r_d N_t\left(1 - \frac{N_t}{K}\right)$$

- **The discrete population growth model has a built in time lag of 1.0 (i.e. intergeneration time)**
  - **In continuous growing population, lag effects are influenced by the product of rate of increase and time lag(*rτ*).**
  - **In discrete population, time lag is 1, so dynamics of pop growth are essentially a function of discrete growth factor (r_d)**

Discrete Population Growth – Logistic Models

$$N_{t+1} = N_t + r_d N_t \left(1 - \frac{N_t}{K}\right)$$

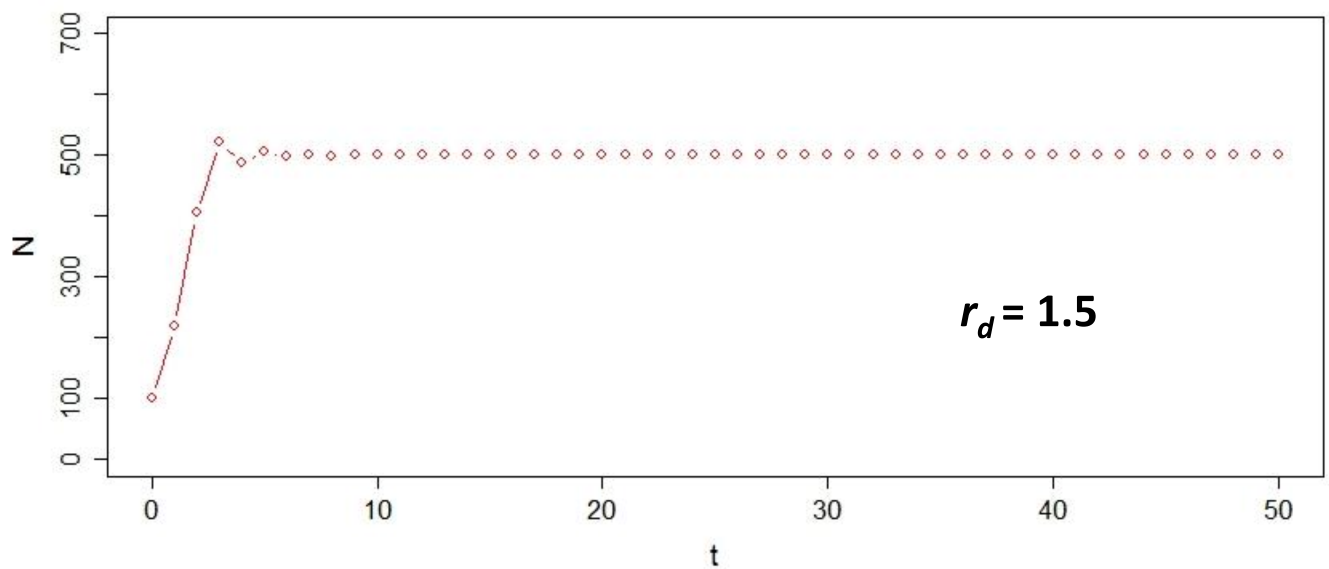



```
t <- seq(1,50,1)
N0 <- 100
rd  <- 0.4
K <- 500

N <- seq(0,length(t),1)
N[1]<-N0

for(ts in t){
  N[ts+1]  <- N[ts]  + rd*N[ts]*(1-(N[ts]/K))
}
```

Discrete Population Growth – Logistic Models

- **Dynamics of Discrete Population**

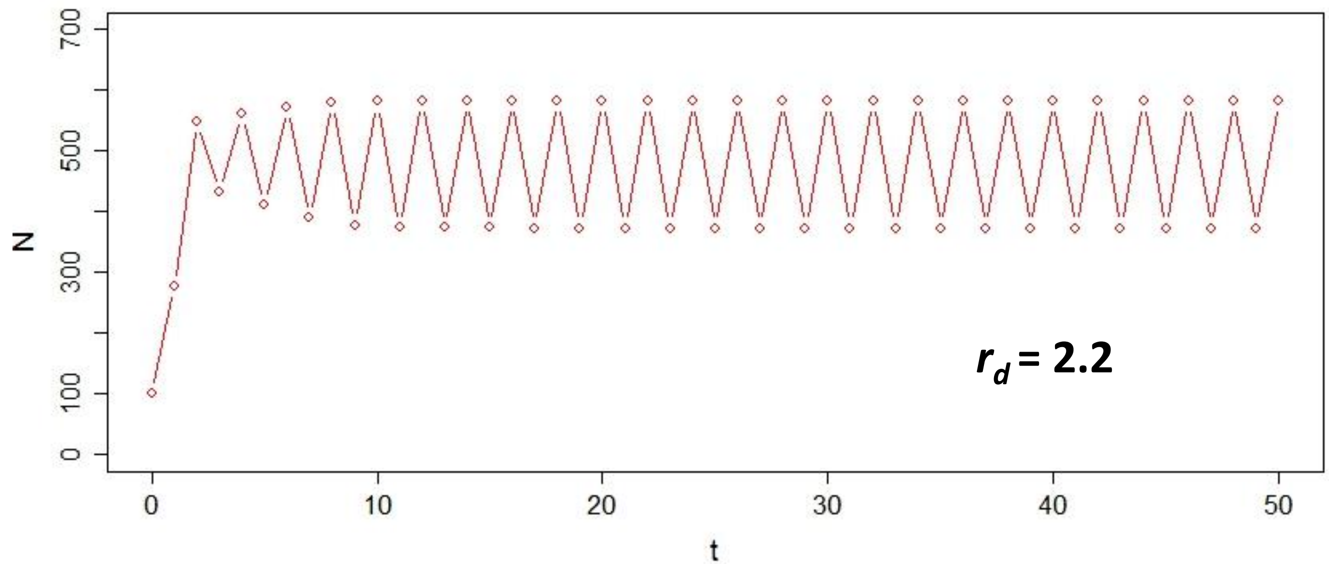
1. **If the Discrete Growth Factor is small (r_d<2.0), then you get dampened oscillations to a stable population at K**



Discrete Population Growth – Logistic Models

- **Dynamics of Discrete Population**

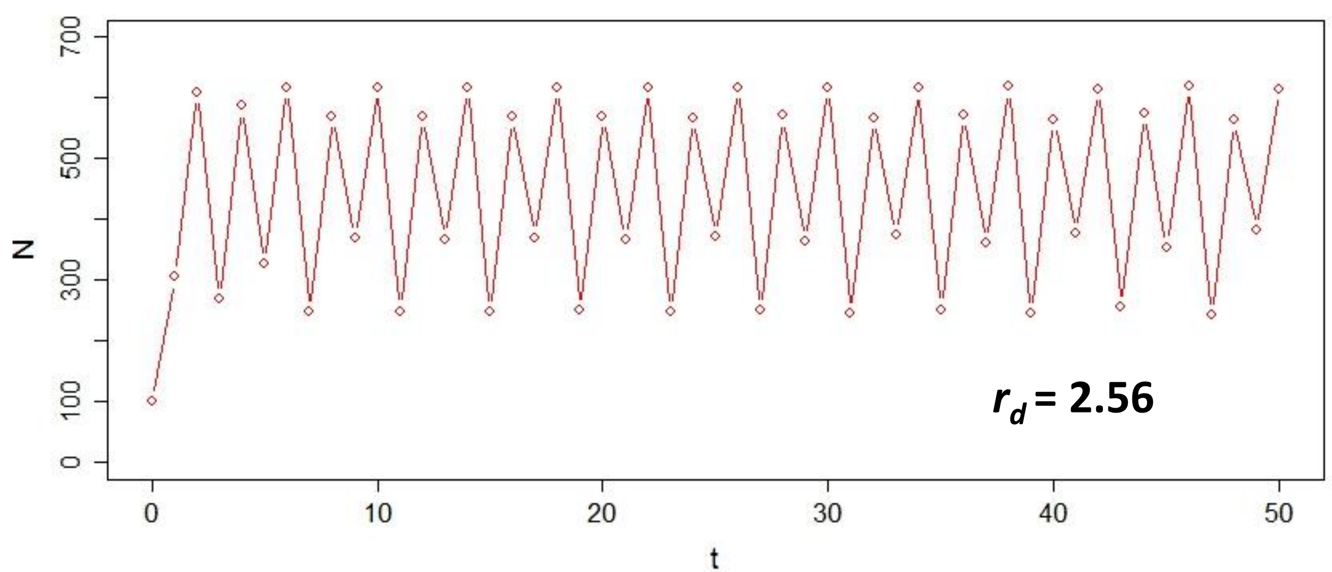
2. If the Discrete Growth Factor is a bit larger (r_d >2.0 but less than 2.449), then you get stable two-point limit cycles.



Discrete Population Growth – Logistic Models

- **Dynamics of Discrete Population**

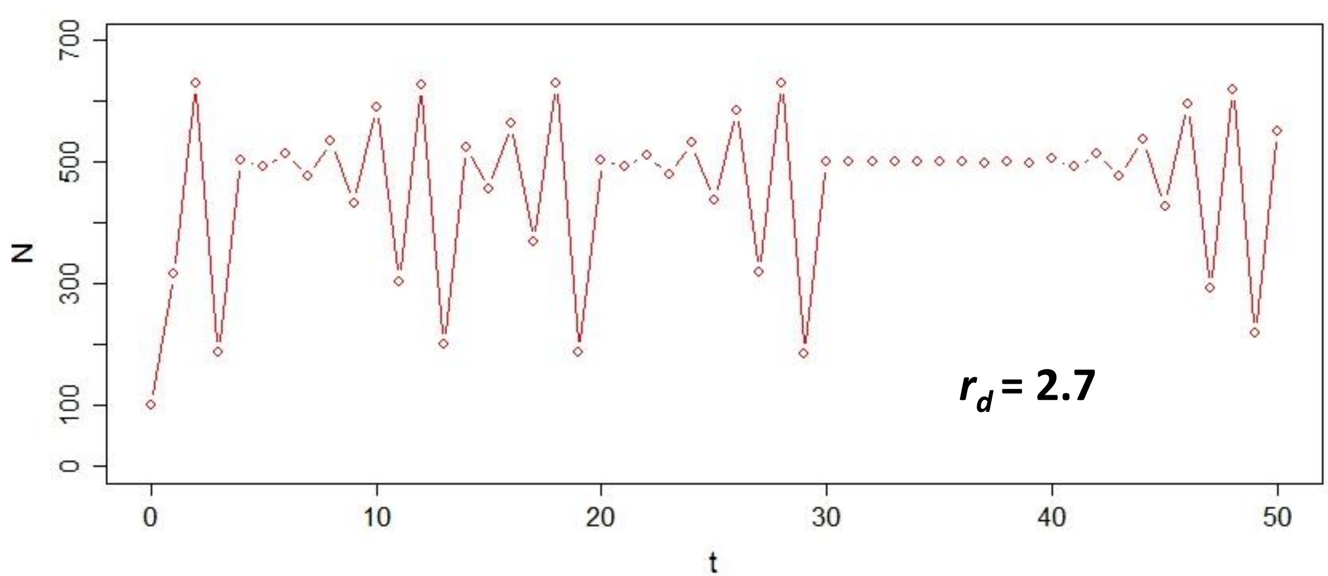
3. **When the Discreet Growth Factor is between 2.449 to 2.570 (2.449<r_d>2.57), you get growth with complex limit cycles, with varying number of “points”.**



Discrete Population Growth – Logistic Models

- **Dynamics of Discrete Population**

4. **When the Discreet Growth Factor is above 2.570, the limit cycles break down and the population grows in a non-repeating pattern (*chaos*)**



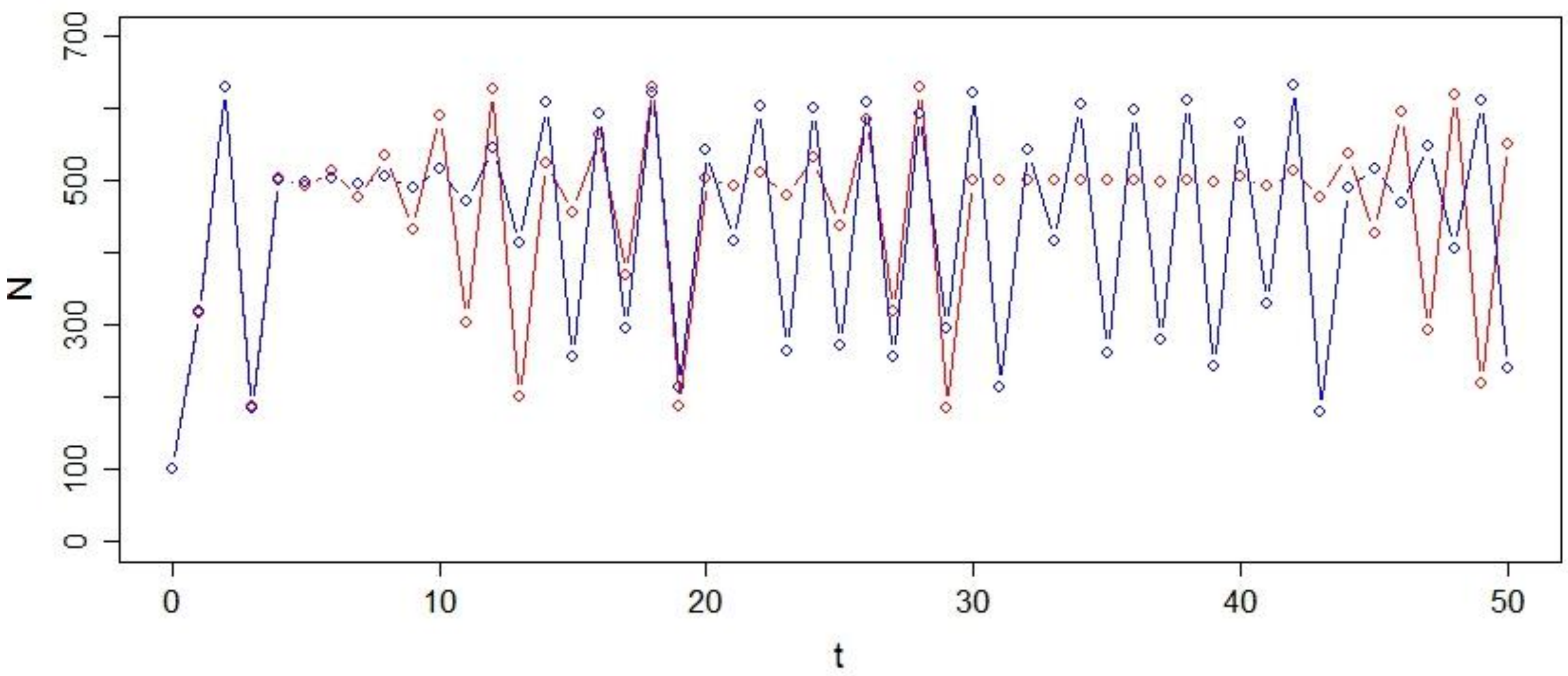
Discrete Population Growth – Logistic Models

- **Chaos vs Stochasticity**

r_d = 2.7

N_0 = 100

N_0= 101



Variation in Carrying Capacity

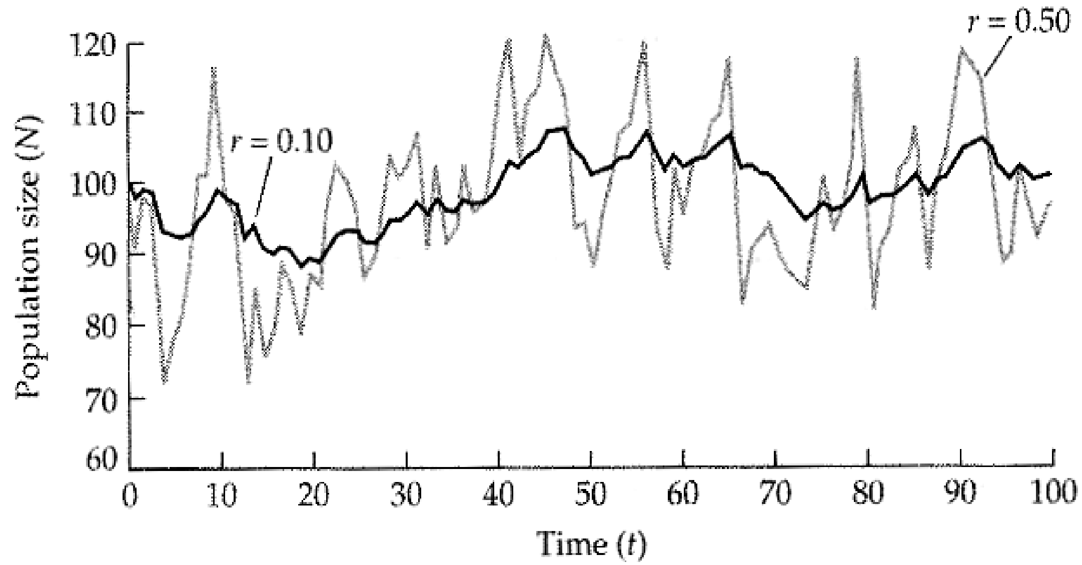
- **Environmental Variation may cause carrying capacity to change over time**
- **Variation could be:**
    1. **Random**
    2. **Cyclic**

Variation in Carrying Capacity

- **Random Variation in Carrying Capacity (K)**
- **If *r* is not variable, but carrying capacity changes over time, result is complex growth patterns**
- **When a population is above the carrying capacity, it declines at a faster rate than it will increase if it is at a corresponding similar point *below* the carrying capacity.**
- **If the carrying capacity is described by a mean ($\bar{K}$) with an associated variance (σ_K^2), a rough approximation of the mean population size will be:**
  - $\bar{N} = \bar{K} - \frac{\sigma_K^2}{2}$

Variation in Carrying Capacity

- **Random Variation in Carrying Capacity (K)**
  - **The more variable the environment, the smaller the average population size.**
  - **If the intrinsic rate of increase (*r*) is large, the population closely tracks changes in carrying capacity.**



  - **if the small intrinsic rate of increase (*r*) is small, the population do not fluctuate much in size as carrying capacity varies, but the population size (N) will tend to be overall somewhat smaller than a population that has a rapid intrinsic growth rate.**

Variation in Carrying Capacity

- **Periodic (cyclic) variation in Carrying Capacity**
- **e.g. seasonal variation in resources**

- $K_t = k_0 + k_1 \cos\left(\frac{2\pi t}{c}\right)$
- K_t = carrying capacity at time t
- k_0 = is mean carrying capacity
- k_1 = the amplitude of the cycle
- c = the length of the cycle

Variation in Carrying Capacity

- **Periodic (cyclic) variation in Carrying Capacity**
- **length of the cycle acts as a time lag, so the behavior of the model depends on the factor *rc* (as it did previously with *rτ*)**

Variation in Carrying Capacity

- **if rc is large (>>1.0), then the population tends to track the fluctuations in the environment:**
- $\boldsymbol{N_t \approx k_0 + k_1 \cos(\frac{2\pi t}{c})}$
- **If rc is very small (<<1.0), then the population tends to average out the fluctuations and persist at a level slightly below carrying capacity**
- $\boldsymbol{\bar{N} \approx \sqrt{k_0^2 - k_t^2}}$