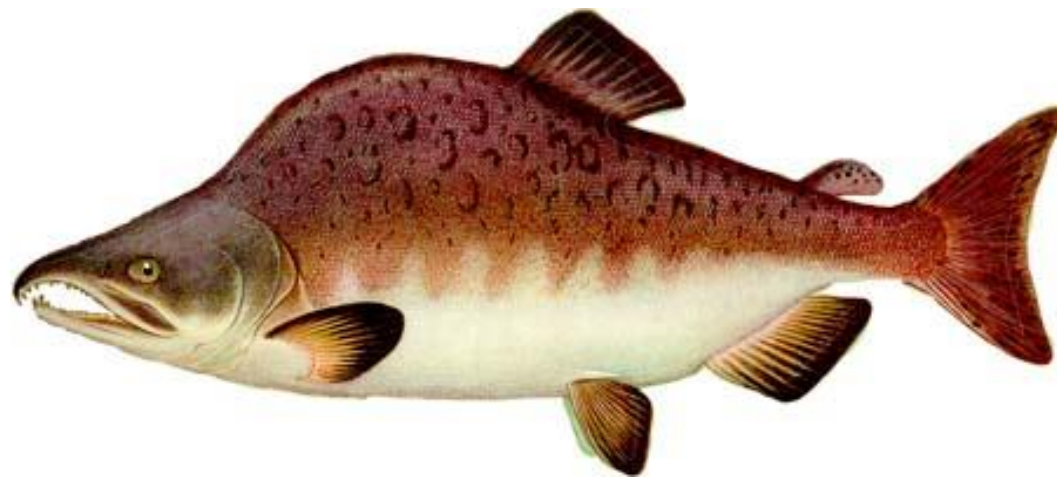


# Complex Population Dynamics

# Quiz

Which of the following are plausible reasons for the non-cycling of salmon populations?

- (a) Insufficient harvesting
- (b) High harvesting
- (c) Lack of severe density dependence
- (d) Presence of severe density dependence



# Concepts

- Population cycling
- Overcompensation
- Bifurcation
- Aperiodic dynamics
- Cobweb diagram
- Dynamics of age-structured populations

# Population dynamics in *Parus*

## Detecting density dependence:

1. Compare vital rates (birth/death/movement) to abundance

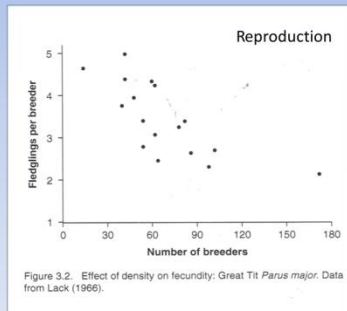
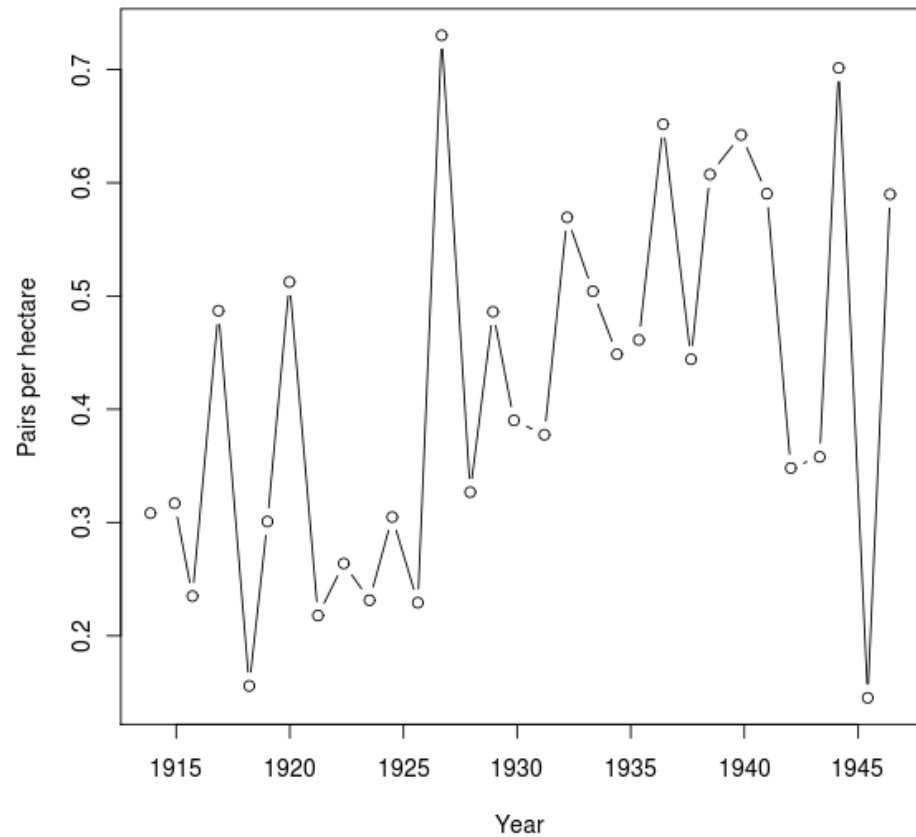
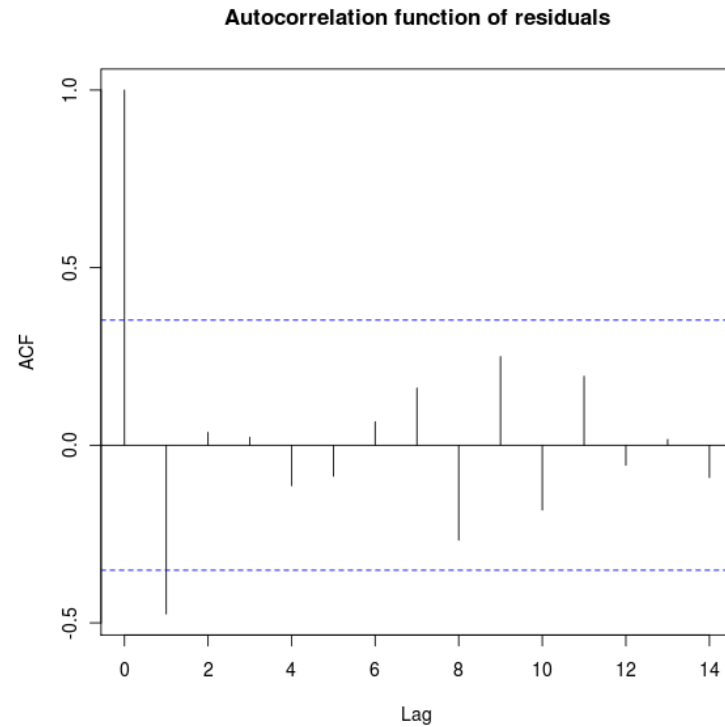
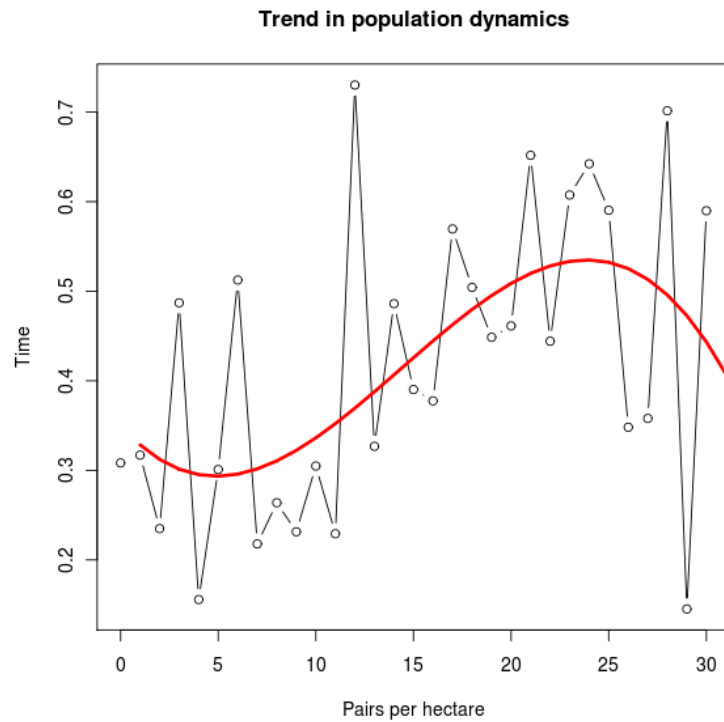


Figure 3.2. Effect of density on fecundity. Great Tit *Parus major*. Data from Lack (1966).

How would you describe these data?

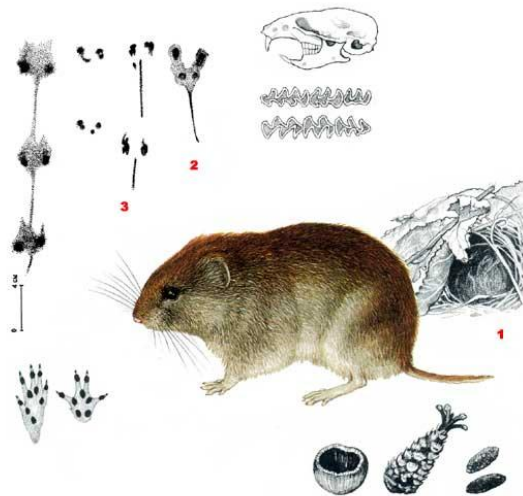


# Is this population cycling?

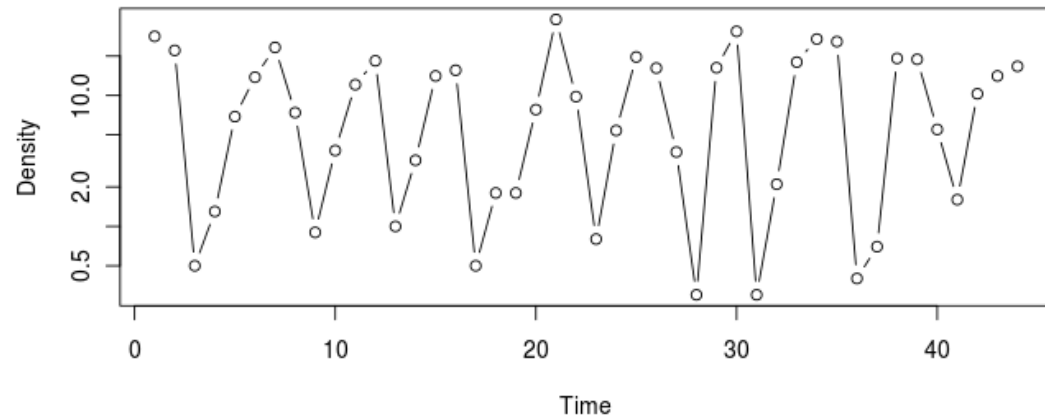


*Parus major* populations appear to be *cycling* around a moving baseline carrying capacity

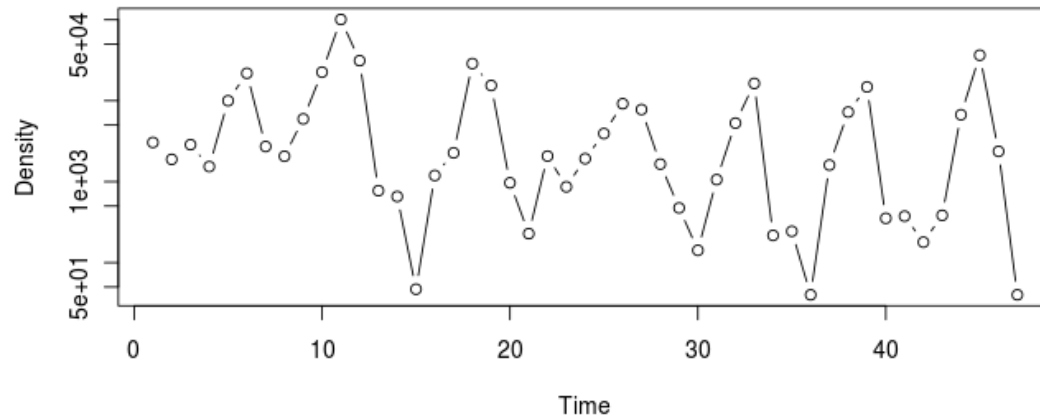
# Are there other classes of dynamical phenomena?



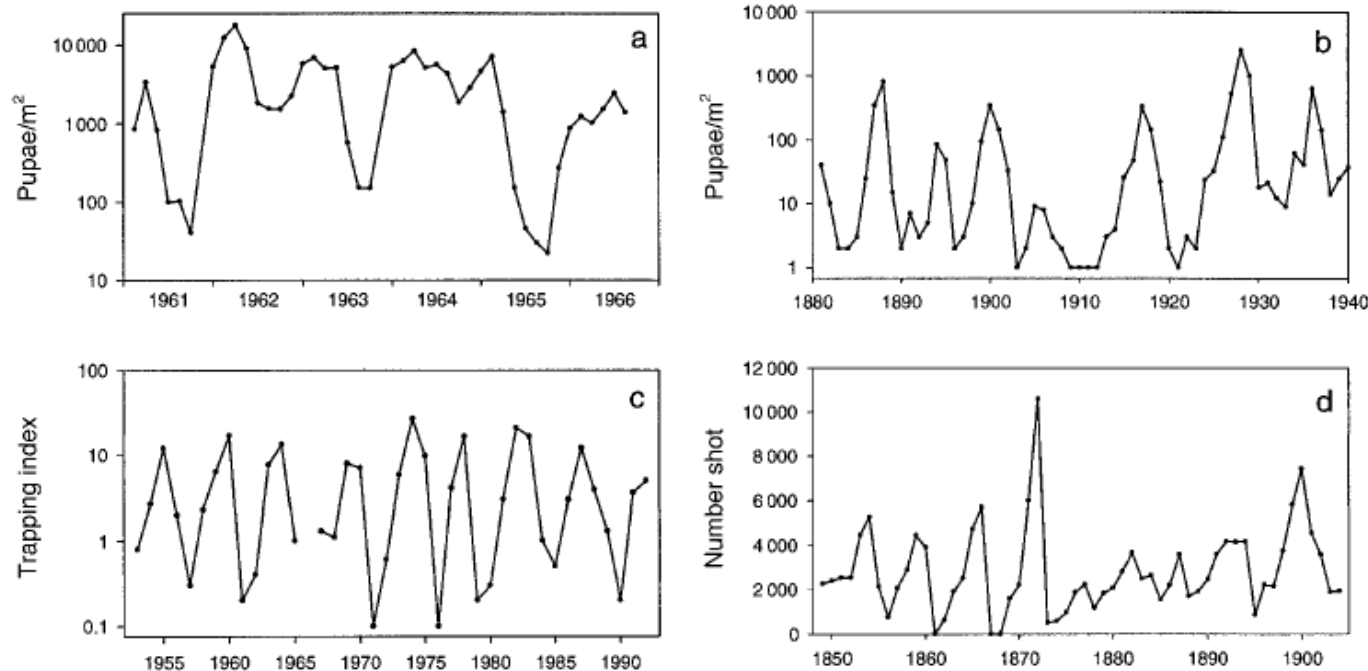
Grey Red-backed Vole (*Clethrionomys rufocanus*)



Water Vole (*Arvicola terrestris*)



# Frequency of Cyclical Dynamics



From Kendall et al. (1999) Ecology 80: 1789-1805.

30% of long term time series exhibit periodic oscillations

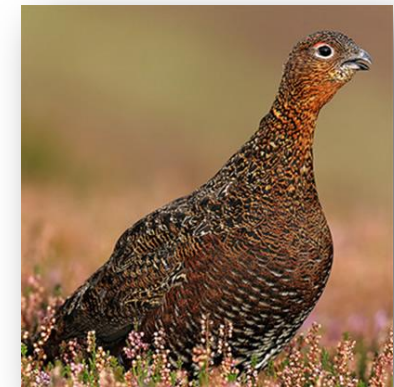
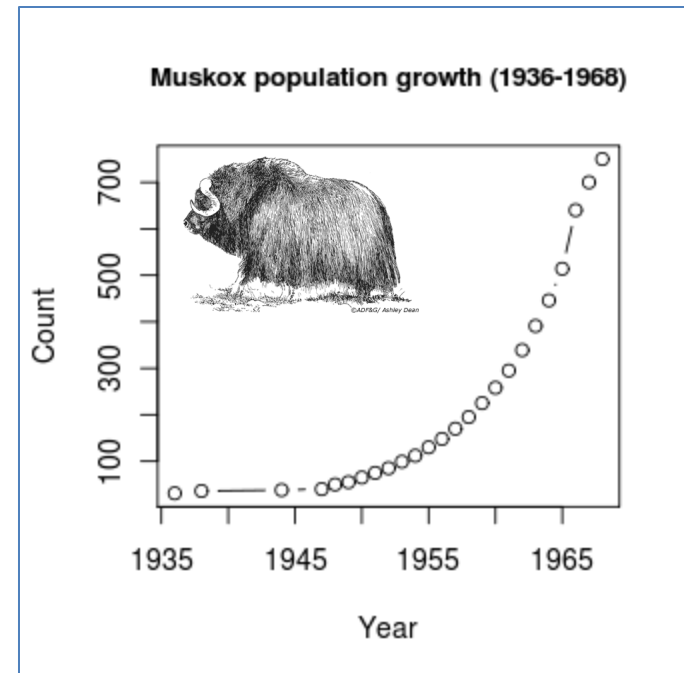
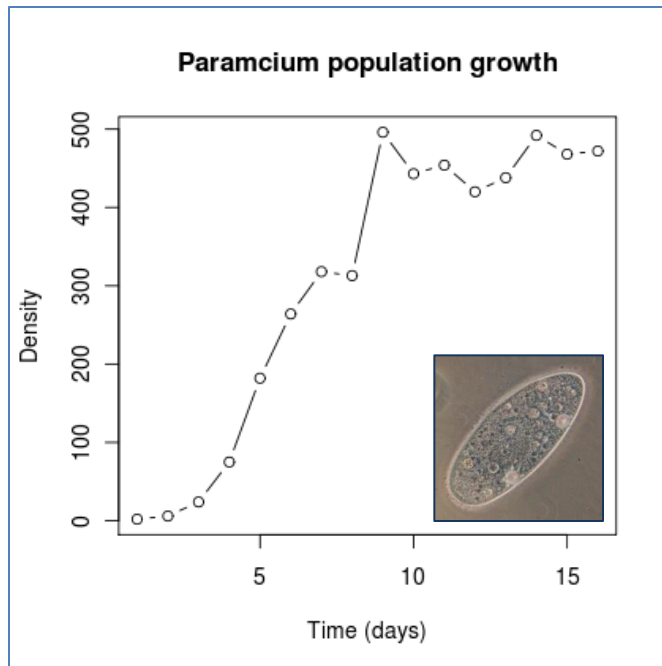


FIG. 1. Examples of cyclic population dynamics. (a) Coffee leaf-miners (*Leucoptera* spp.) at Lyamungu, Tanzania (Bigger 1973). (b) Pine looper (*Bupalus piniarius*) in Germany (Schwerdtfeger 1941). (c) Voles (*Microtus* and *Clethrionomys*) at Kilpisjärvi, northern Finland (Laine and Henttonen 1983, Hanski et al. 1993). (d) Red Grouse (*Lagopus lagopus scoticus*) in Scotland (Middleton 1934).

# What causes populations to cycle?

- Classes of population dynamics
  - Exponential/geometric growth
  - Exponential/geometric decline
  - Equilibrium (carrying capacity)
  - Equilibrium (extinction)





# Density dependence redux

$$\lambda(N) = \frac{R}{1 + aN_t}$$

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

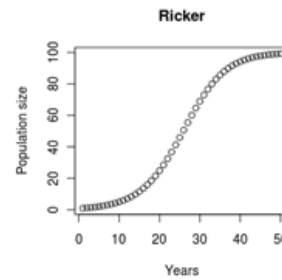
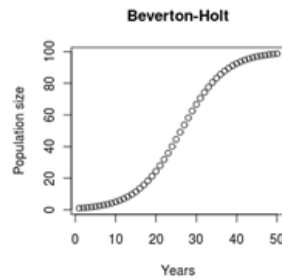
$$\lambda(N) = \lambda_0 e^{bN_t}$$

$$N_{t+1} = N_t \lambda_0 e^{bN_t}$$

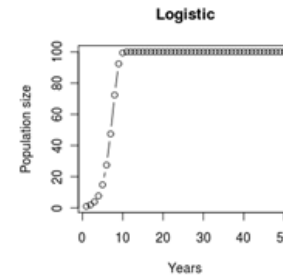
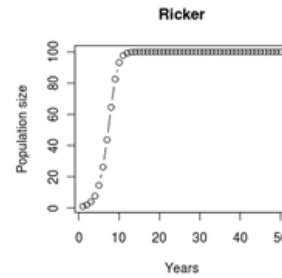
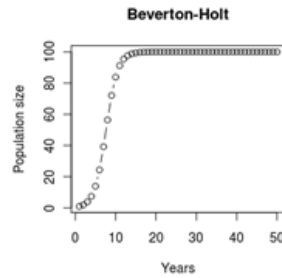
$$\lambda(N) = R(1 - N/K)$$

$$N_{t+1} = N_t R(1 - N/K)$$

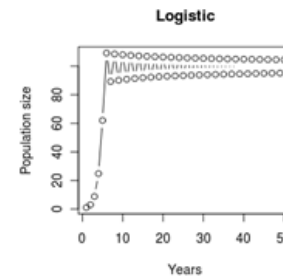
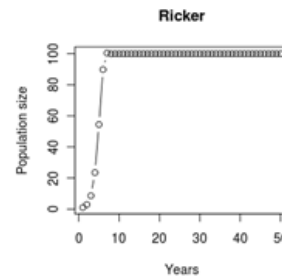
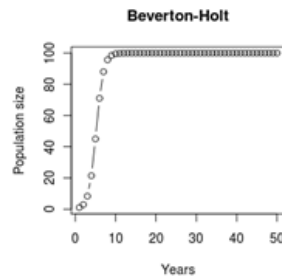
$R=1.2$



$R=2.0$



$R=3.0$



# Overcompensation

Overcompensation occurs when populations with periodic reproduction “overshoot” carrying capacity

$$\lambda(N) = \frac{R}{1 + aN_t}$$

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

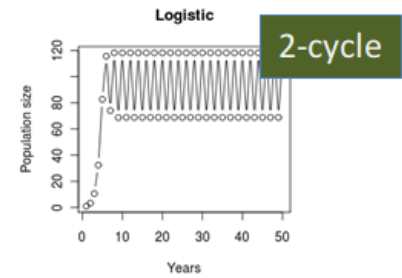
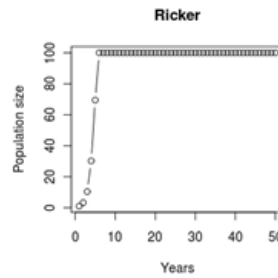
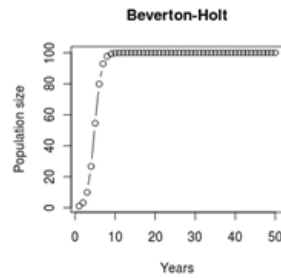
$$\lambda(N) = \lambda_0 e^{bN_t}$$

$$N_{t+1} = N_t \lambda_0 e^{bN_t}$$

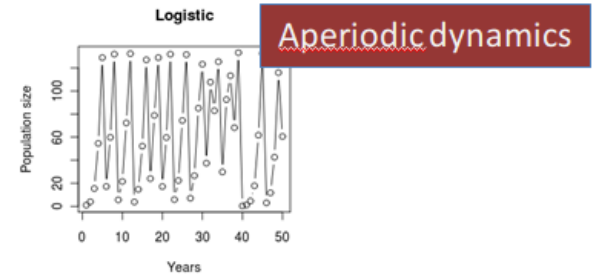
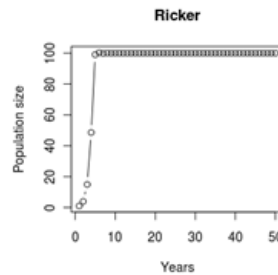
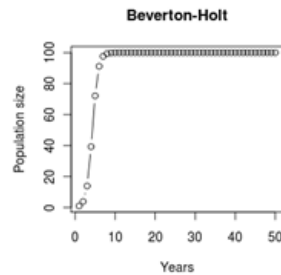
$$\lambda(N) = R(1 - N/K)$$

$$N_{t+1} = N_t R(1 - N/K)$$

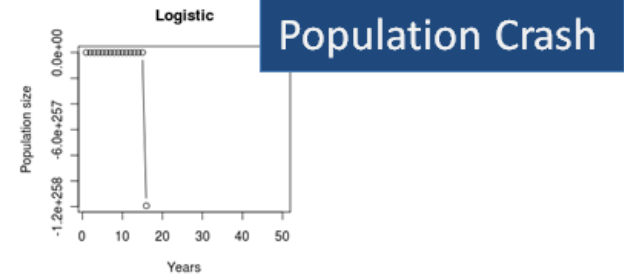
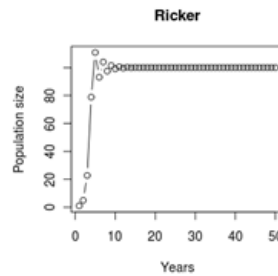
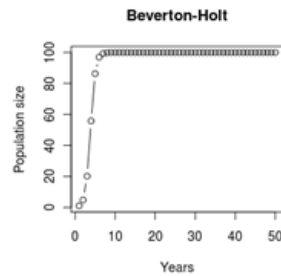
R=3.2



R=4.0



R=5.0



# Overcompensation

$$\lambda(N) = \frac{R}{1 + aN_t}$$

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

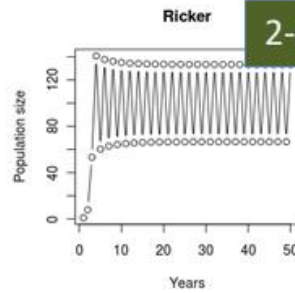
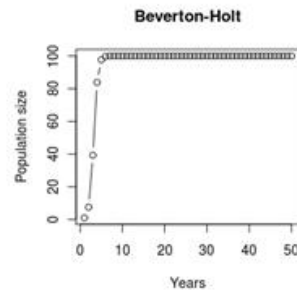
$$\lambda(N) = \lambda_0 e^{bN_t}$$

$$N_{t+1} = N_t \lambda_0 e^{bN_t}$$

$$\lambda(N) = R(1 - N/K)$$

$$N_{t+1} = N_t R(1 - N/K)$$

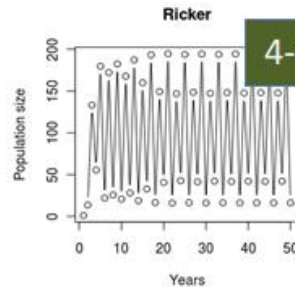
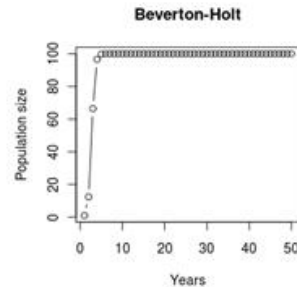
$R=8.0$



2-cycle



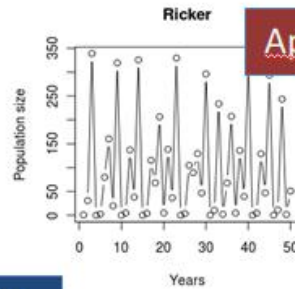
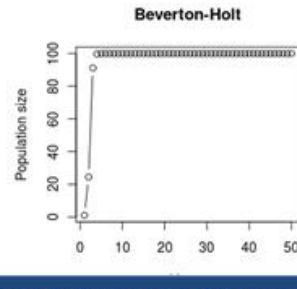
$R=14.0$



4-cycle



$R=32.0$

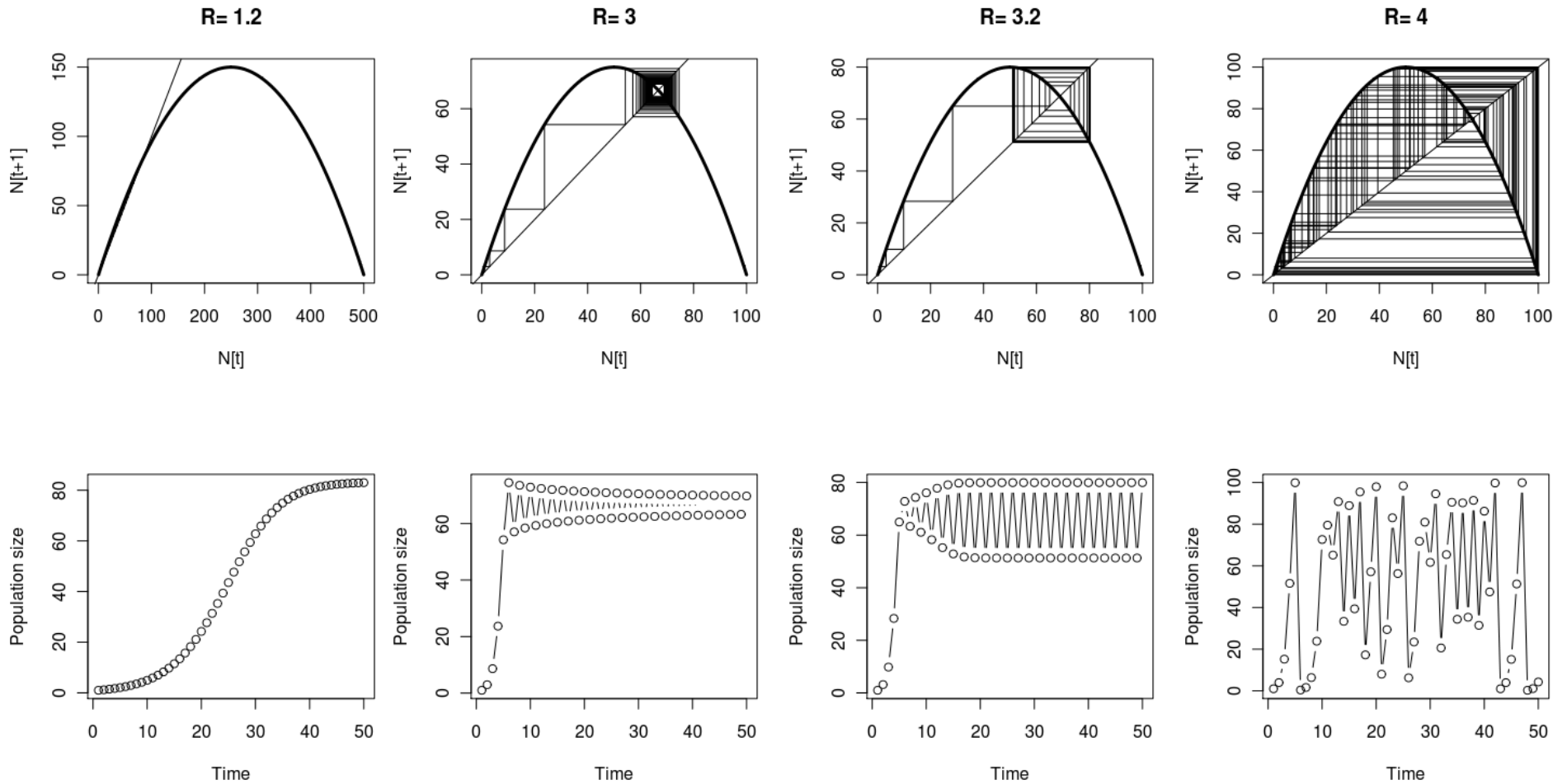


Aperiodic dynamics



Beverton-Holt model always exhibits smooth dynamics

# Cobweb diagrams for the discrete logistic model



# Bifurcation diagram

$$x_{t+1} = (1 + r)x - \frac{rx^2}{k}$$

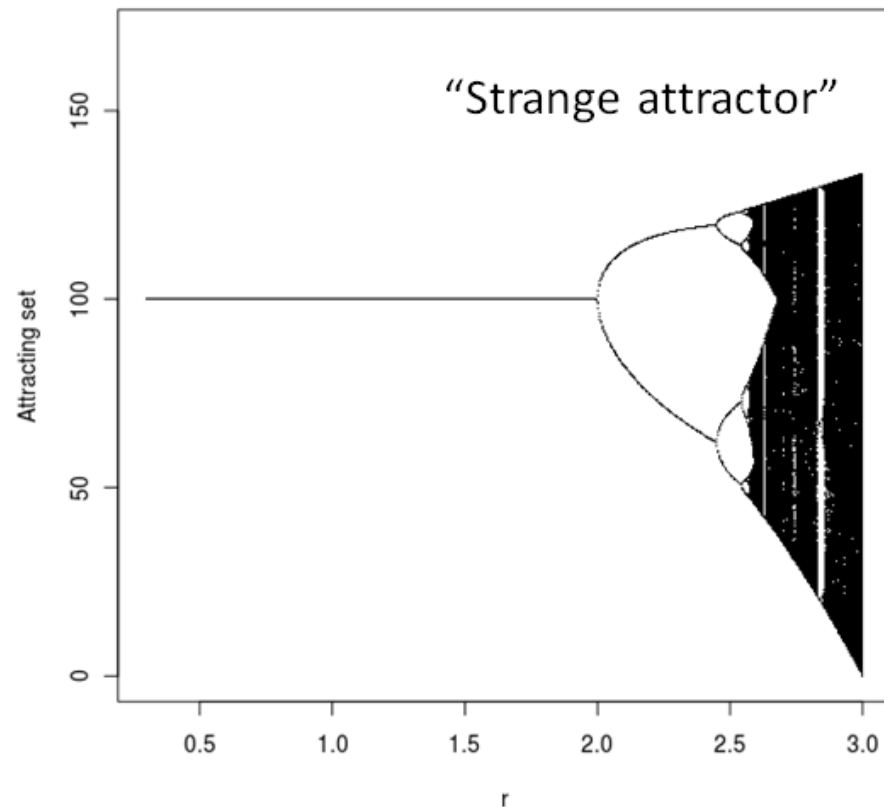
Bifurcation in 1-D maps

- saddle-node bifurcations
- transcritical bifurcations
- pitchfork bifurcations
- period-doubling bifurcations

Aperiodic behavior

Frequency locking

A “bifurcation” occurs when a smooth change in the parameters gives rise to a qualitative change in the long-run population dynamics

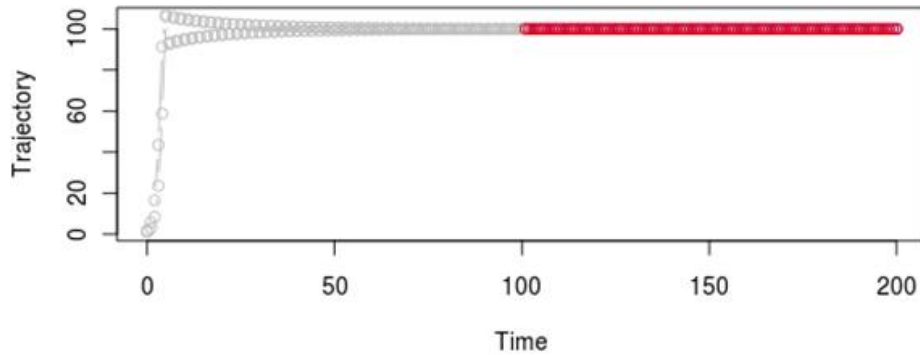


# Dynamical chaos

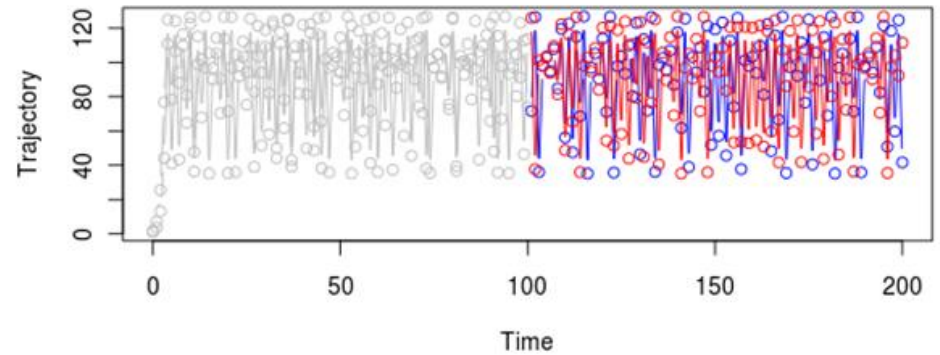
- Dynamical chaos is one kind of *aperiodic behavior* (population trajectory never repeats itself)
  - A candidate explanation for fluctuations in nature
- Characterized by *sensitivity to initial conditions*
- Fully deterministic, but nearly *indistinguishable from random noise*
- Characteristics predisposing a population to chaos include:
  - Annualized reproduction (or time lags)
  - High reproductive output
  - High nonlinearity

# Sensitive dependence on initial conditions (“lyapunov exponent”)

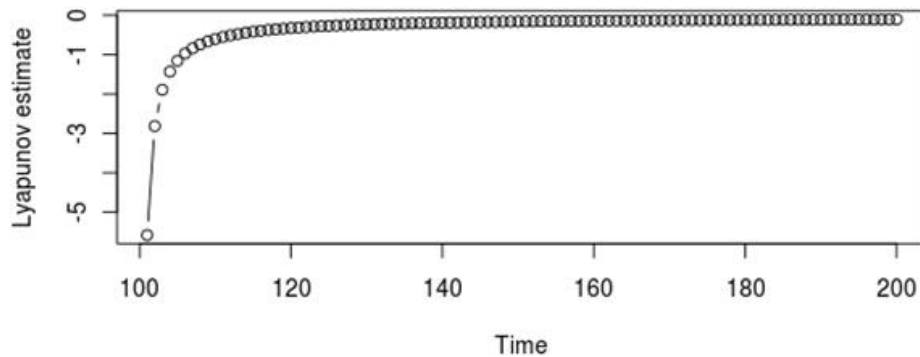
**r = 1.95**



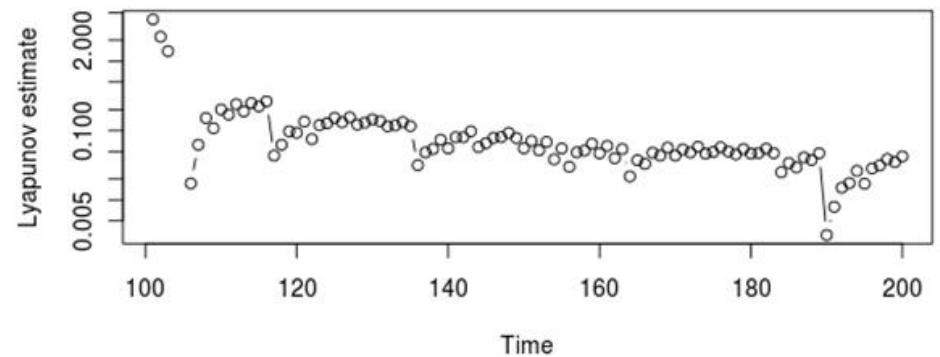
**r = 2.7**



**r = 1.95**



**r = 2.7**



$$\lambda = \lim_{n \rightarrow \infty} \frac{1}{n} \sum_{i=0}^{n-1} \log \left( \left| \frac{df}{dx}(x_i) \right| \right)$$

## Stability analysis of discrete time models

- Step 1. Let  $x^*$  be an equilibrium of the model. Define a new abstract quantity,  $u$ , to be a small perturbation away from  $x^*$ . We will ask the question, “Does  $u$  grow or shrink?”

$$u(t) = x(t) - x^*$$

- Step 2. Rewrite the dynamical system model using  $u$

$$x_{t+1} = f(x_t)$$

becomes

$$x^* + u_{t+\Delta t} = f(x^* + u_t)$$



## Stability analysis of discrete time models

### Taylor's Theorem

$$f(x^*) + \frac{f'(x^*)}{1!}(x-x^*)^1 + \frac{f''(x^*)}{2!}(x-x^*)^2 + \frac{f'''(x^*)}{3!}(x-x^*)^3 + \dots$$

- Step 3. Linearize using Taylor's theorem

$$x^* + u_{t+\Delta t} = f(x^*) + uf'(x)_{x=x^*}$$

$x^*$  on l.h.s. cancels with  $f(x^*)$  on r.h.s. and we have an equation for the growth of our perturbation

$$u_{t+\Delta t} = uf'(x)_{x=x^*}$$

#### Rules for stability

- If  $f'(x) > 1$  : geometric growth
- If  $0 < f'(x) < 1$  : geometric decline
- If  $-1 < f'(x) < 0$  : damped oscillations
- If  $f'(x) < -1$  : divergent oscillations

## Example with discrete logistic model

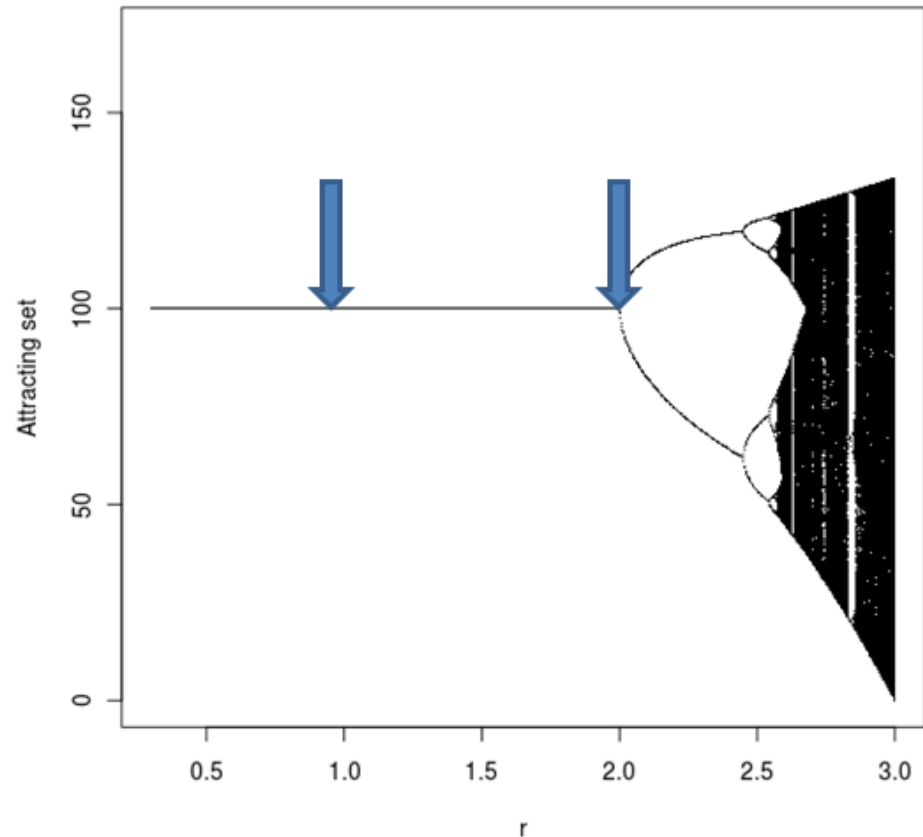
$$x_{t+1} = (1-r)x - \frac{rx^2}{k}$$

$$f'(x) = 1 + r - 2x \frac{r}{k}$$

$$f'(x=k) = 1 + r + 2x^* \frac{r}{x^*}$$

$$f'(x=k) = 1 + r - 2r$$

$$f'(x=k) = 1 - r$$



$0 < r < 1$  : geometric decline  
 $1 < r < 2$  : damped oscillations  
 $r > 2$  : divergent oscillations

# Bootstrap estimates of uncertainty by Falck et al. 2005

