

# **Density dependence**

The dependence of a per capita life history parameter on population size or density

Reading: vandermeer and Goldberg p7-19; p28-29

# Logistic growth (continuous time)

- Logistic growth model can be derived assuming
    - $r$  is linearly related to food available
    - Food available is linearly related to population size
- See vandermeer and Goldberg p. 14-17

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

# Logistic growth (continuous time)

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

- $r$ : intrinsic growth rate at low population size (1/time)
- $K$ : carrying capacity (number)
- $N(t)$ : size of the population at time, t.

# Logistic growth (continuous time)

- Per capita growth rate decreases linearly

$$\frac{dN(t)}{dt} = \frac{1}{N(t)}$$

- Has the general solution:

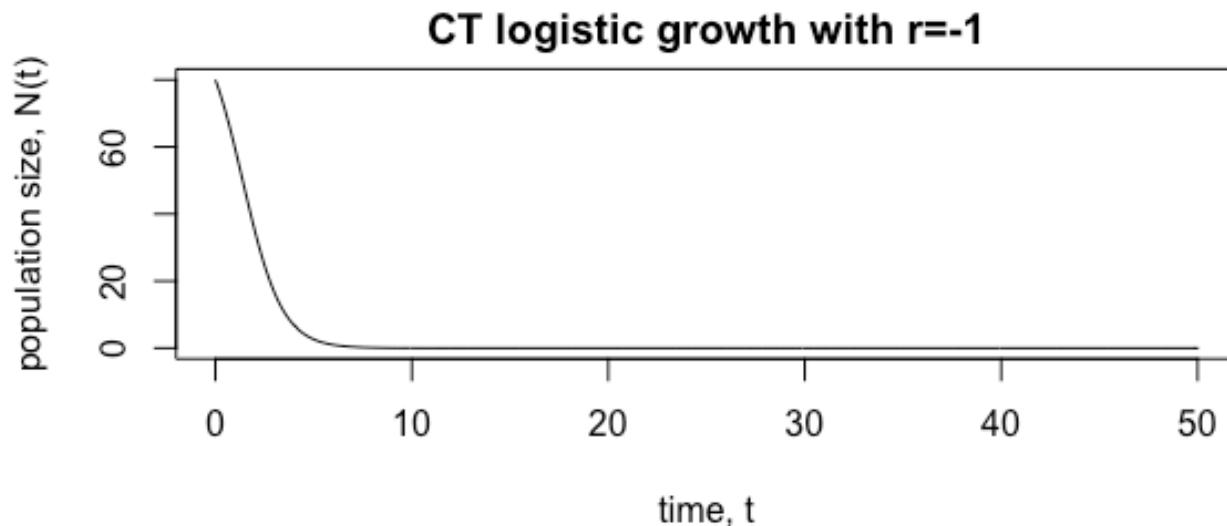
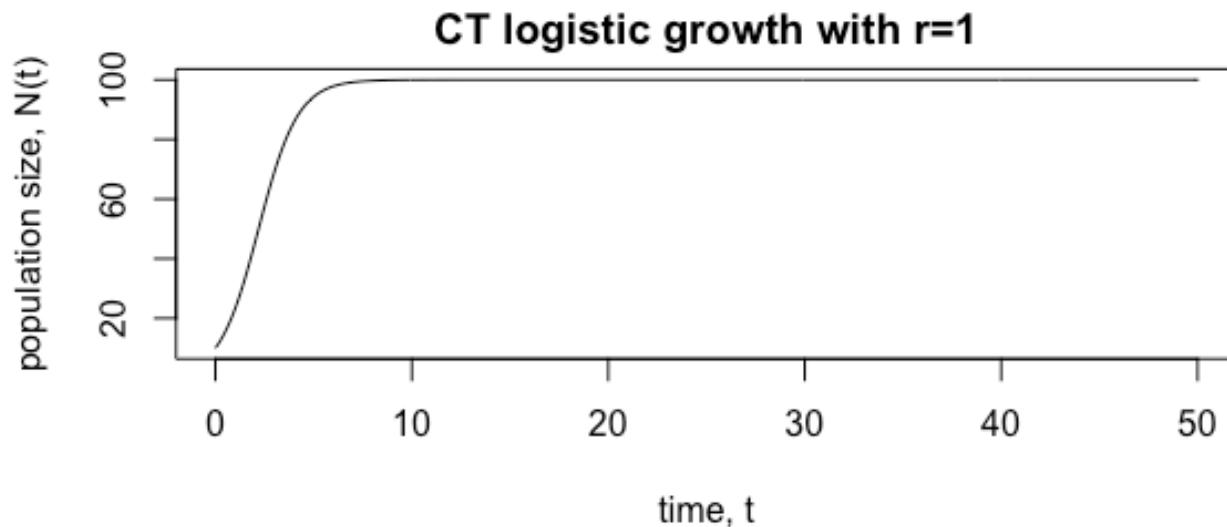
$$N(t) = \frac{KN_0 e^{rt}}{K + N_0(e^{rt} - 1)}$$

see <http://www.math.usu.edu/~powell/ysa-html/node8.html> or differentiate the solution with respect to time to see it satisfies the logistic equation ordinary differential equation. Check  $t=0$  gives  $N_0$ , check  $t$  to infinity

The screenshot shows an RStudio interface with a script editor window titled "DensityDependentGrowth.R". The code in the editor is as follows:

```
1 # SOLVING MODELS FOR DENSITY-DEPENDENT POPULATION GROWTH
2 -----
3 # Models:
4 # 1) Continuous time logistic growth
5 # 2) Discrete time logistic map
6 # 3) Alternative version of the discrete time logistic map
7 # 4) Ricker model (discrete time)
8 # 5) Beverton-Holt model (discrete time)
9
10 # Remove all objects - always start with this
11 rm(list=ls())
12
13 # load the package to numerically solve the continuous time
14 # model
15 require(deSolve)
16
```

# Logistic growth (continuous time)



# Equilibrium points

- Values of  $N(t)$  such that  $\frac{dN(t)}{dt} = 0$
- Equilibria can be unstable
- Stability of equilibrium can be determined by a line-arrow diagram

# Logistic growth (continuous time)

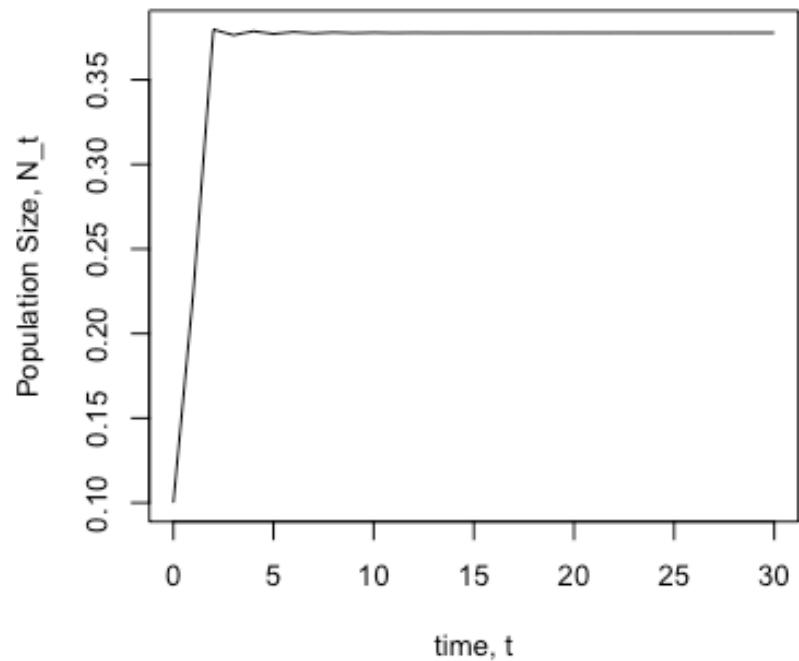
- $N(t) = 0$  is stable when  $r < 0$
- $N(t) = K$  is stable when  $r > 0$

# Logistic growth (discrete time)

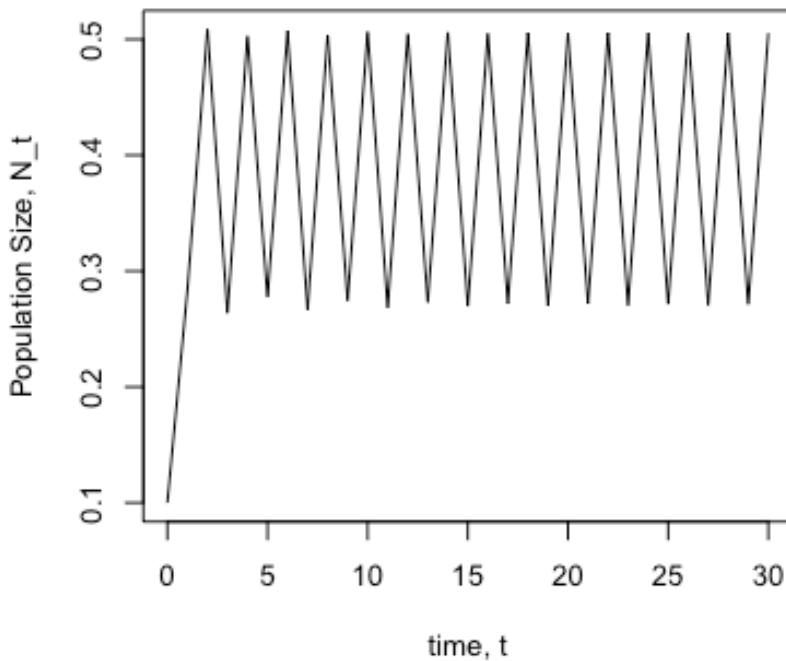
$$\text{May: } N_{t+1} = \lambda N_t \left( \frac{K - N_t}{K} \right)$$

- As from p28 vandermeer and Goldberg. This model has historical significance, but..
- ... this is a poor population model because population size can be negative:
  - i.e. find  $N_1$  and  $N_2$  for  $N_0 = 70$ ,  $K = 100$ , and  $\lambda=5$
- $K$  is not the carrying capacity for this model: the positive equilibrium is  $K(\lambda-1)/\lambda$
- Turchin: *Complex Population Dynamics* has a good discussion of discrete time models with density dependence and their limitations

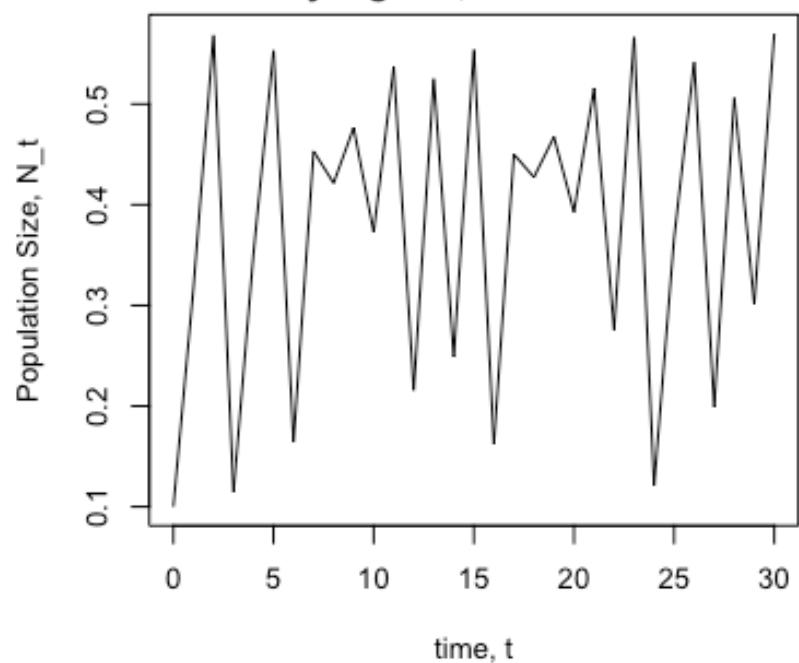
**May logistic, lambda = 2.7**



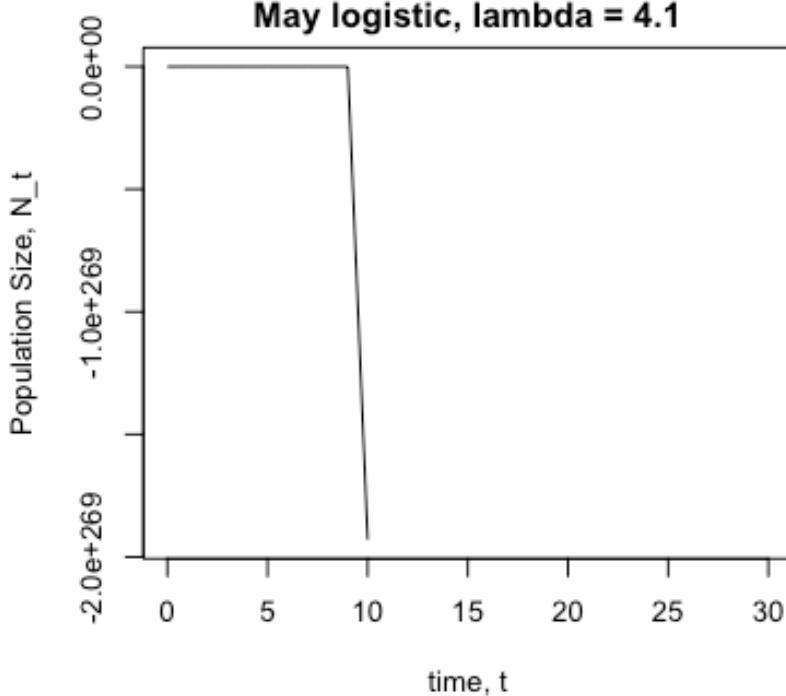
**May logistic, lambda = 3.4**

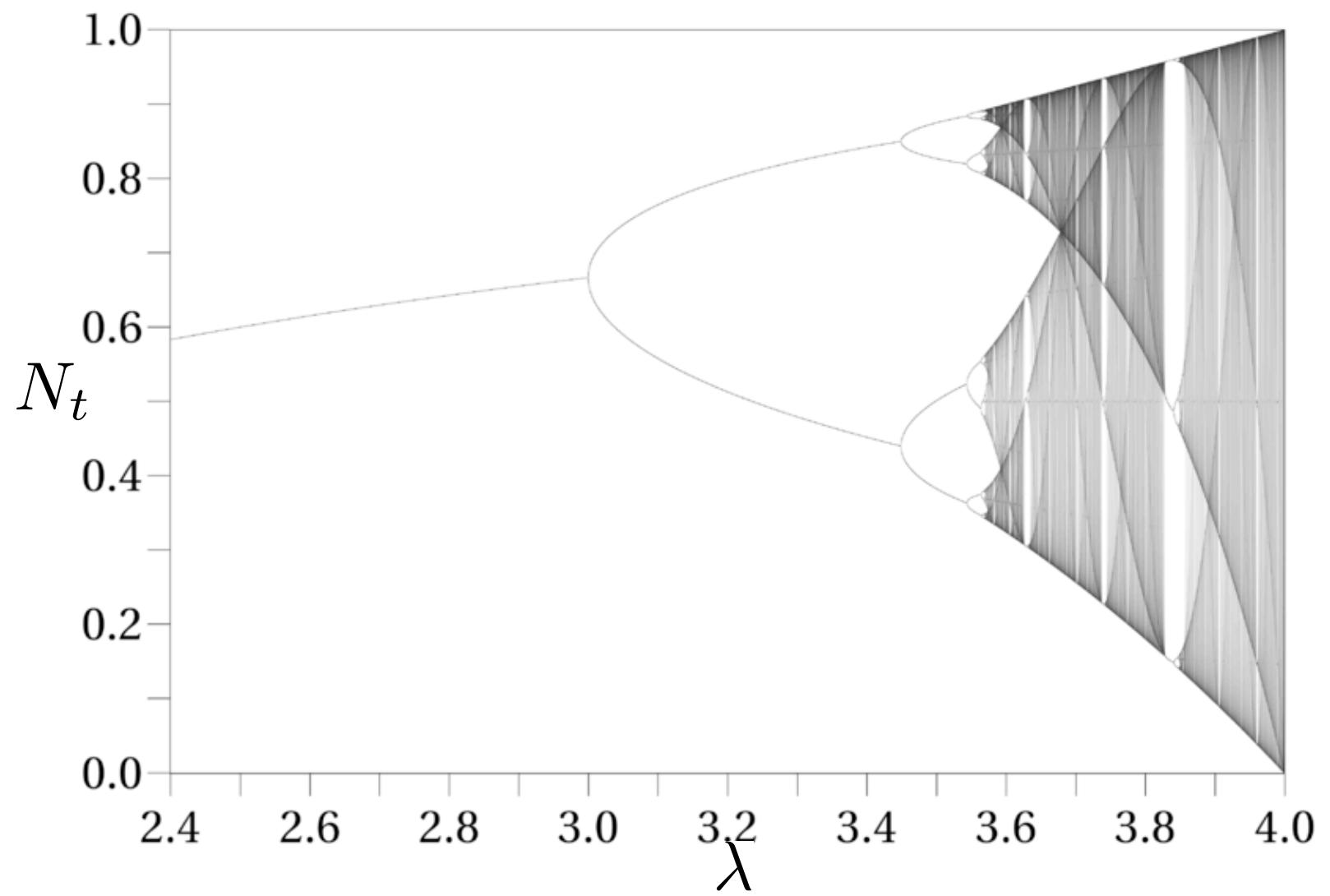


**May logistic, lambda = 3.8**



**May logistic, lambda = 4.1**





# Logistic growth (discrete time)

Alternative formulation:  $N_{t+1} = N_t + \lambda N_t \left( \frac{K - N_t}{K} \right)$

- $K$  is the carrying capacity, but negative values are still possible

# DT Density dependence

Beverton and Holt (1957) model have properties that are similar to the Bleasdale and Nelder formulation, as does the model proposed by Hassell (1975) in the context of a predator–prey model. Indeed, when  $b = 1$ , the Beverton and Holt model is identical to either of the forms of Bleasdale and Nelder, namely,

$$N_{t+1} = \frac{\lambda N_t}{(1 + \alpha N_t)}, \quad (28)$$

and the Hassell model is the same as the first form of the Bleasdale and Nelder model, namely,

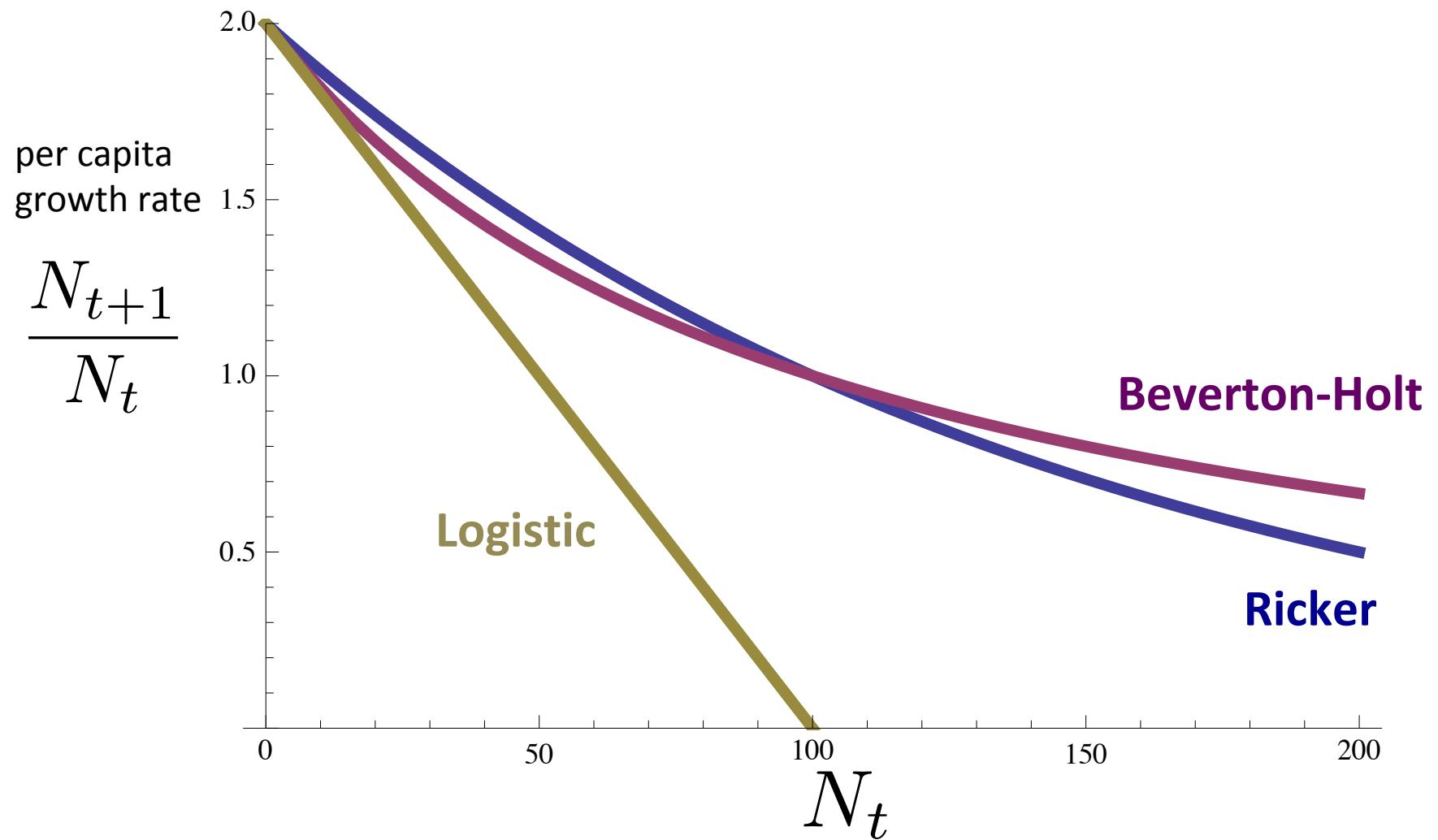
$$N_{t+1} = \frac{\lambda N_t}{(1 + \alpha N_t)^b}. \quad (29)$$

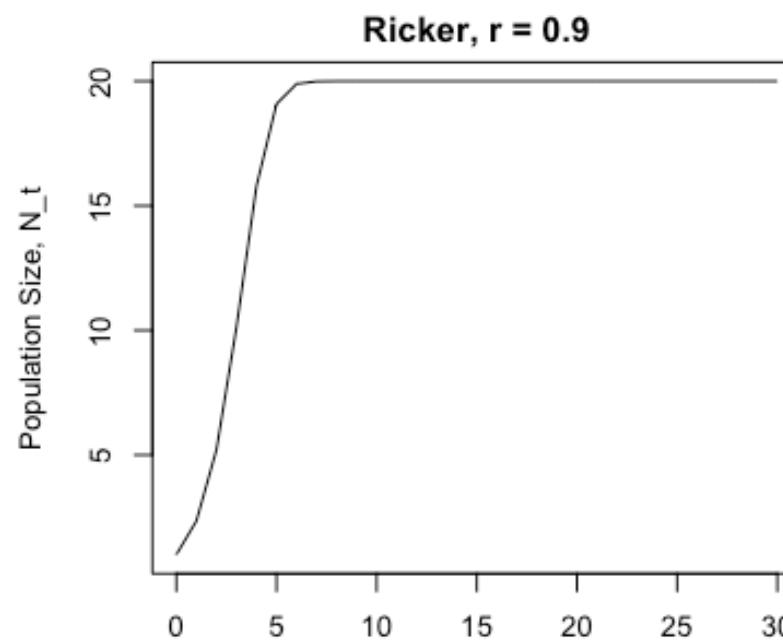
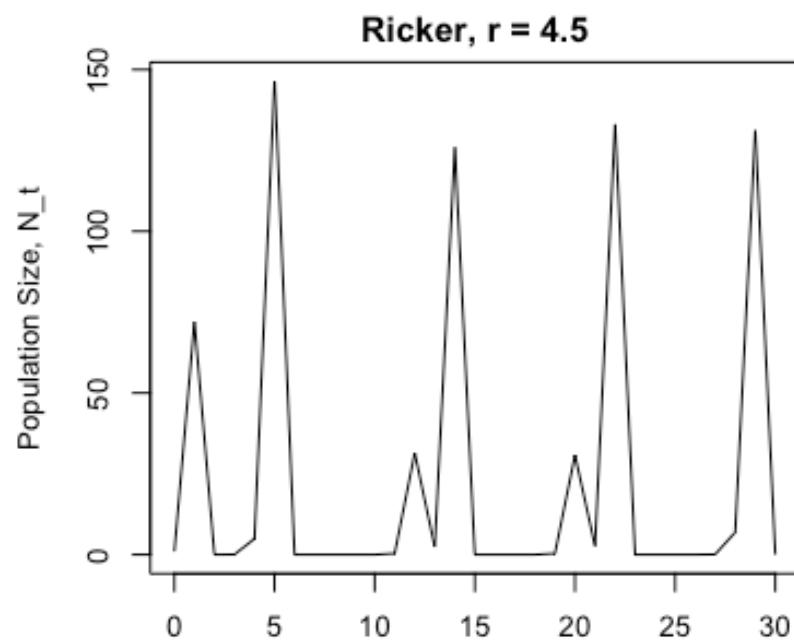
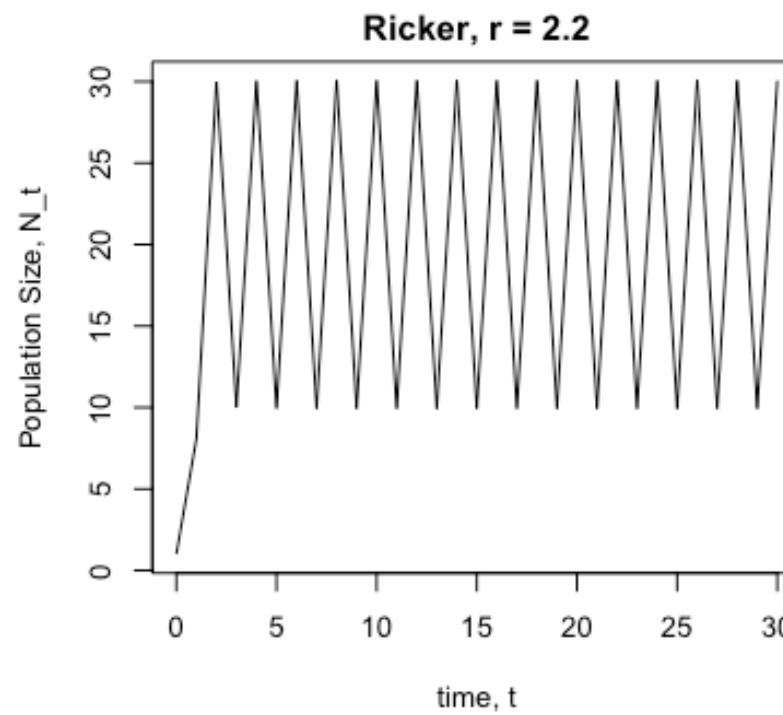
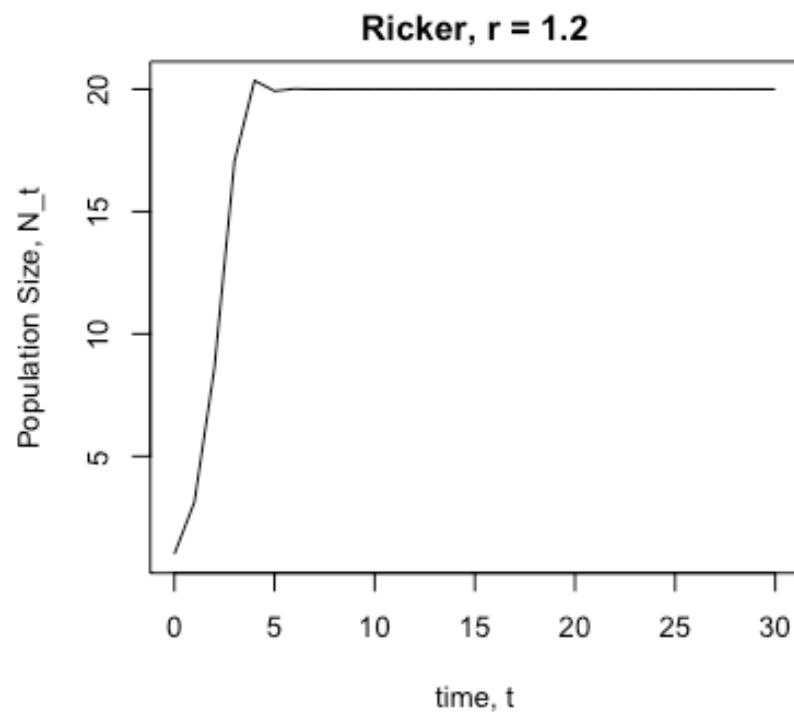
The Ricker model has a similar overall form, although its formulation is exponential, namely,

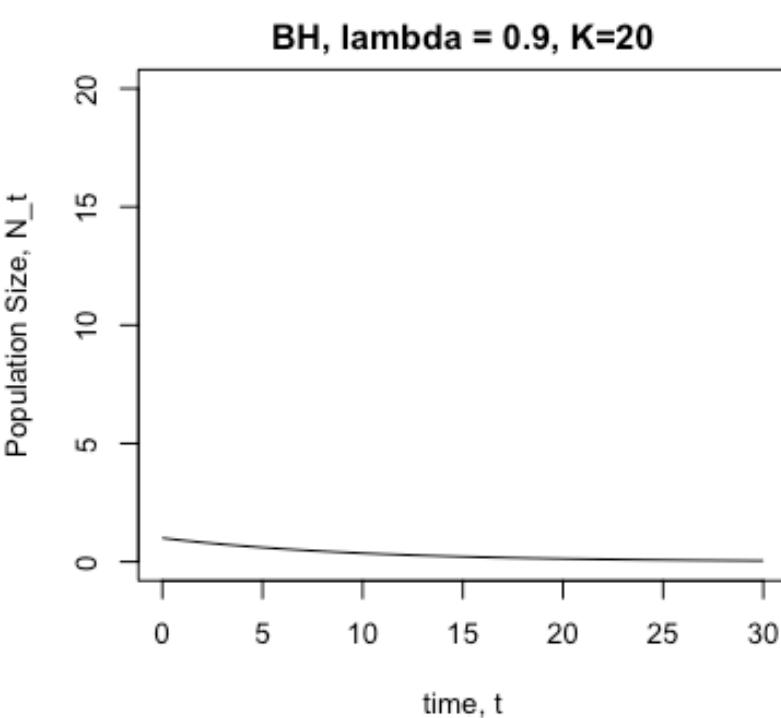
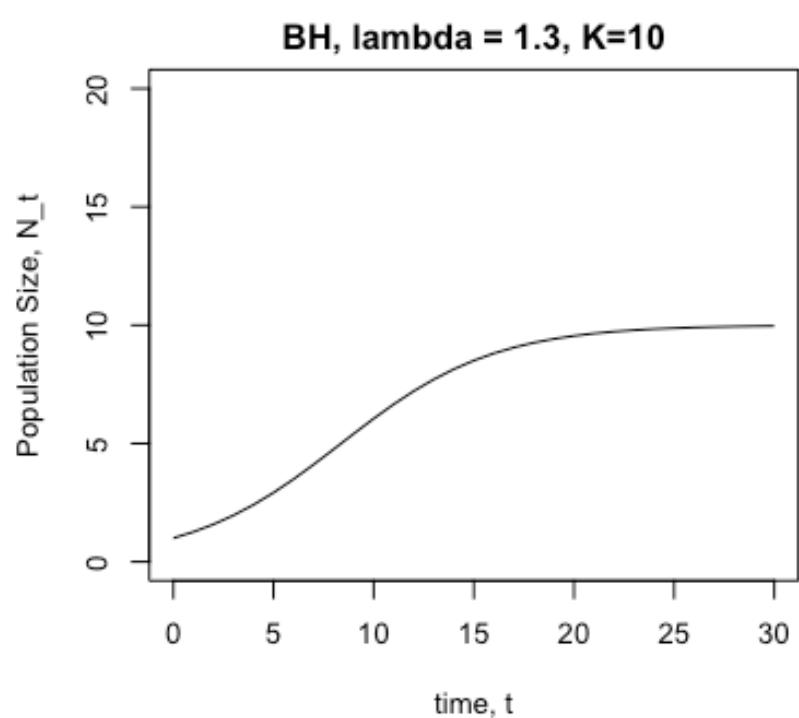
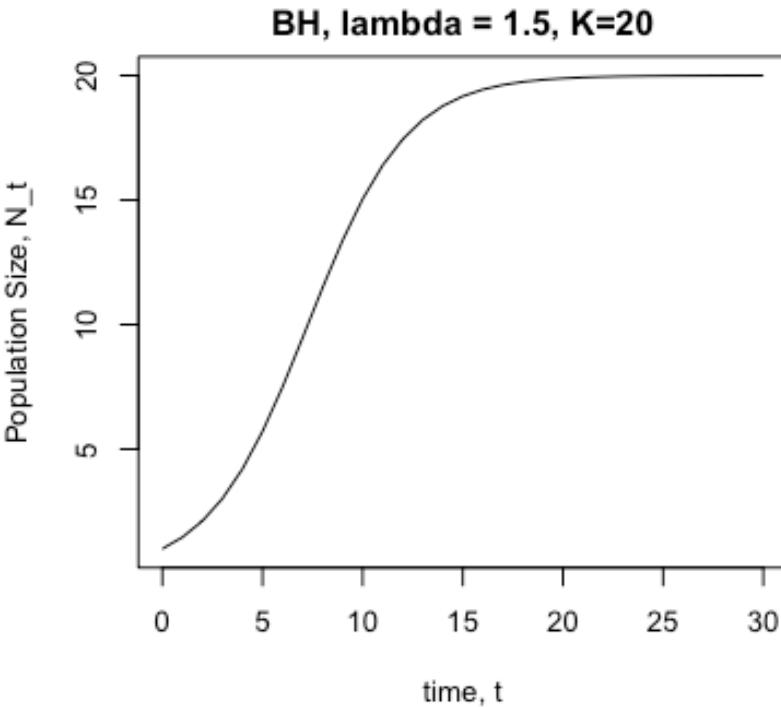
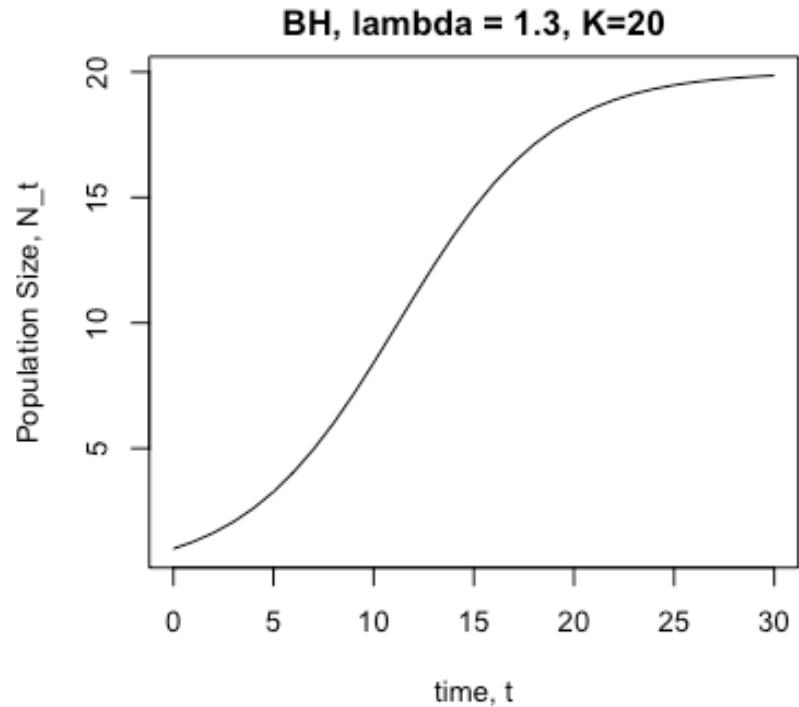
$$N_{t+1} = N_t e^{r(1 - bN_t)}. \quad (30)$$

All have the property that when  $N_{t+1}$  is plotted against  $N_t$  a nonlinear form emerges with a quadratic-like hump, a fact that translates into some interest-

# Discrete time models of density-dependent population growth





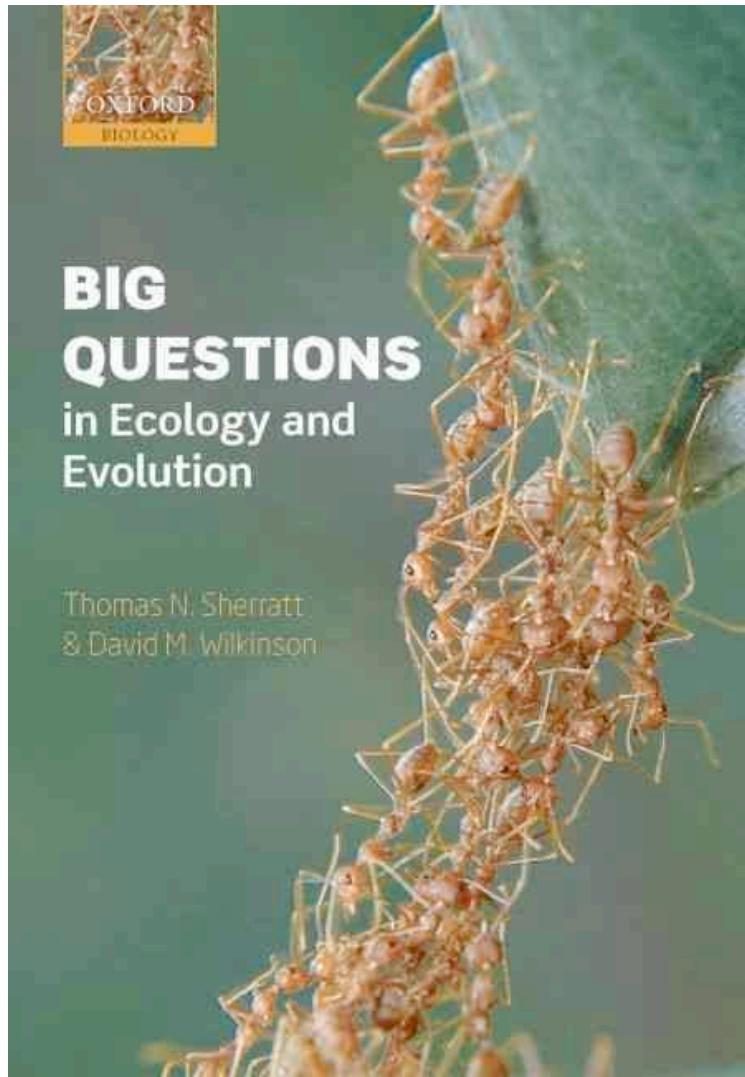


Models	Dynamics
Geometric (DT exponential)	a
CT exponential	a
CT logistic growth	a,b
Alternative DT logistic map	a,b,c,d
Ricker	a,b,c,d
Beverton-Holt	a,b

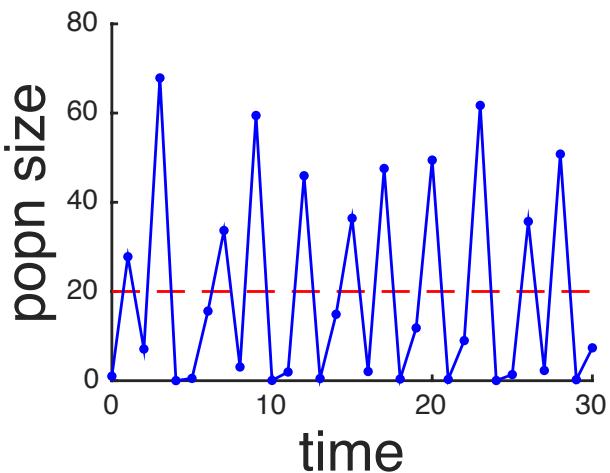
- a. Equilibrium at 0;  
 c. Periodic cycles;

- b. Equilibrium at K;  
 d. Chaos

# Do biological populations exhibit chaotic dynamics?



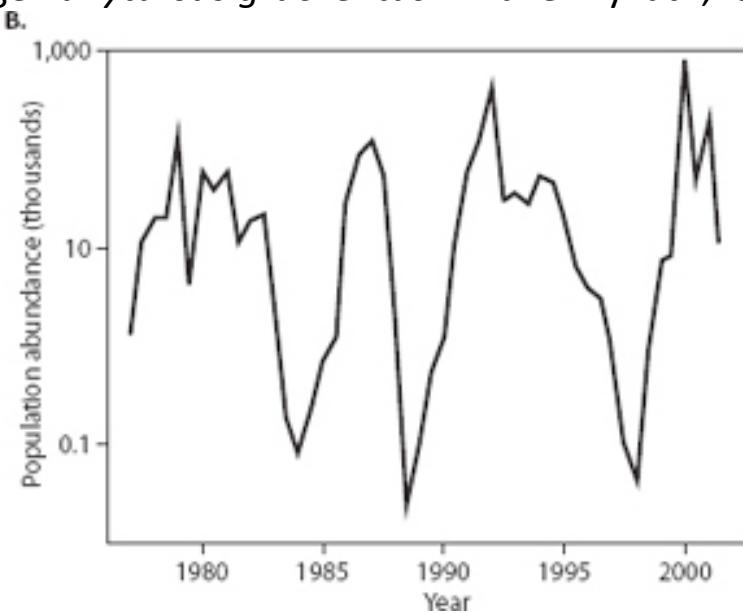
# How to identify chaos?



The midge *Tanytarsus gracilis* in Lake Myvatn, Iceland



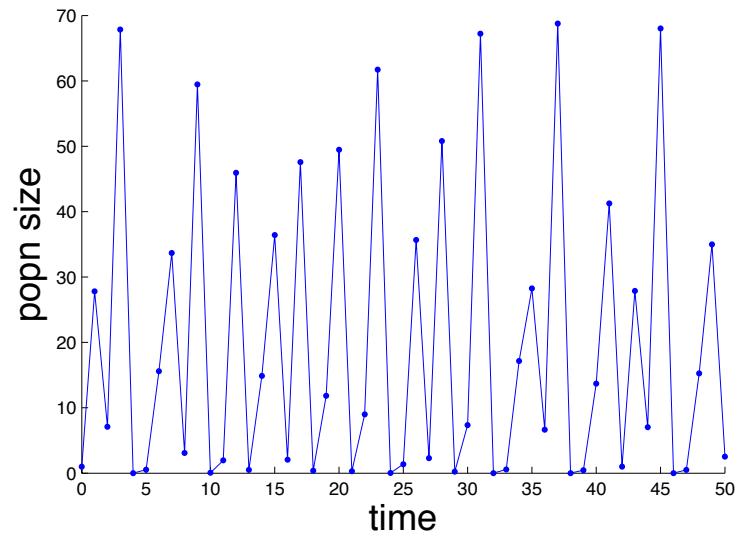
Photo credit: Kenneth Chang



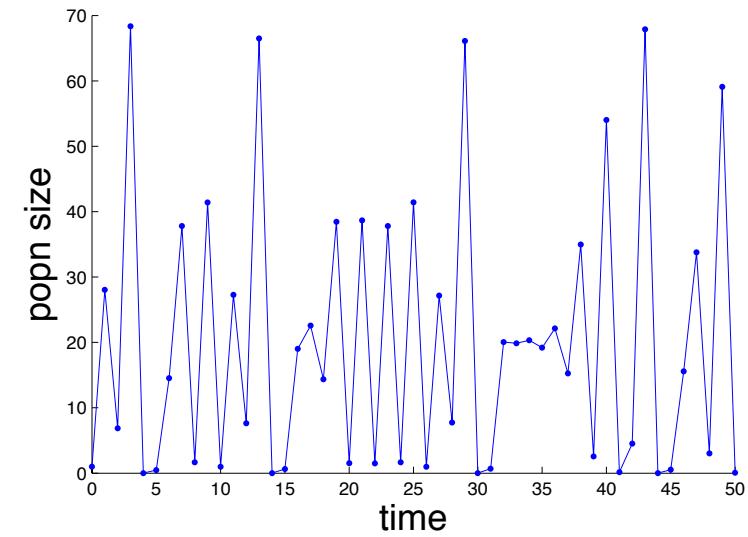
## Definition of chaos

- ‘a trajectory is chaotic if it is bounded in magnitude, neither periodic or approaches a periodic state, and is sensitive to initial conditions’ Cushing et al. 2002. Chaos in ecology. Academic Press.
- Extreme sensitivity to initial conditions – butterfly effect

Initial population size  $N_0 = 1$



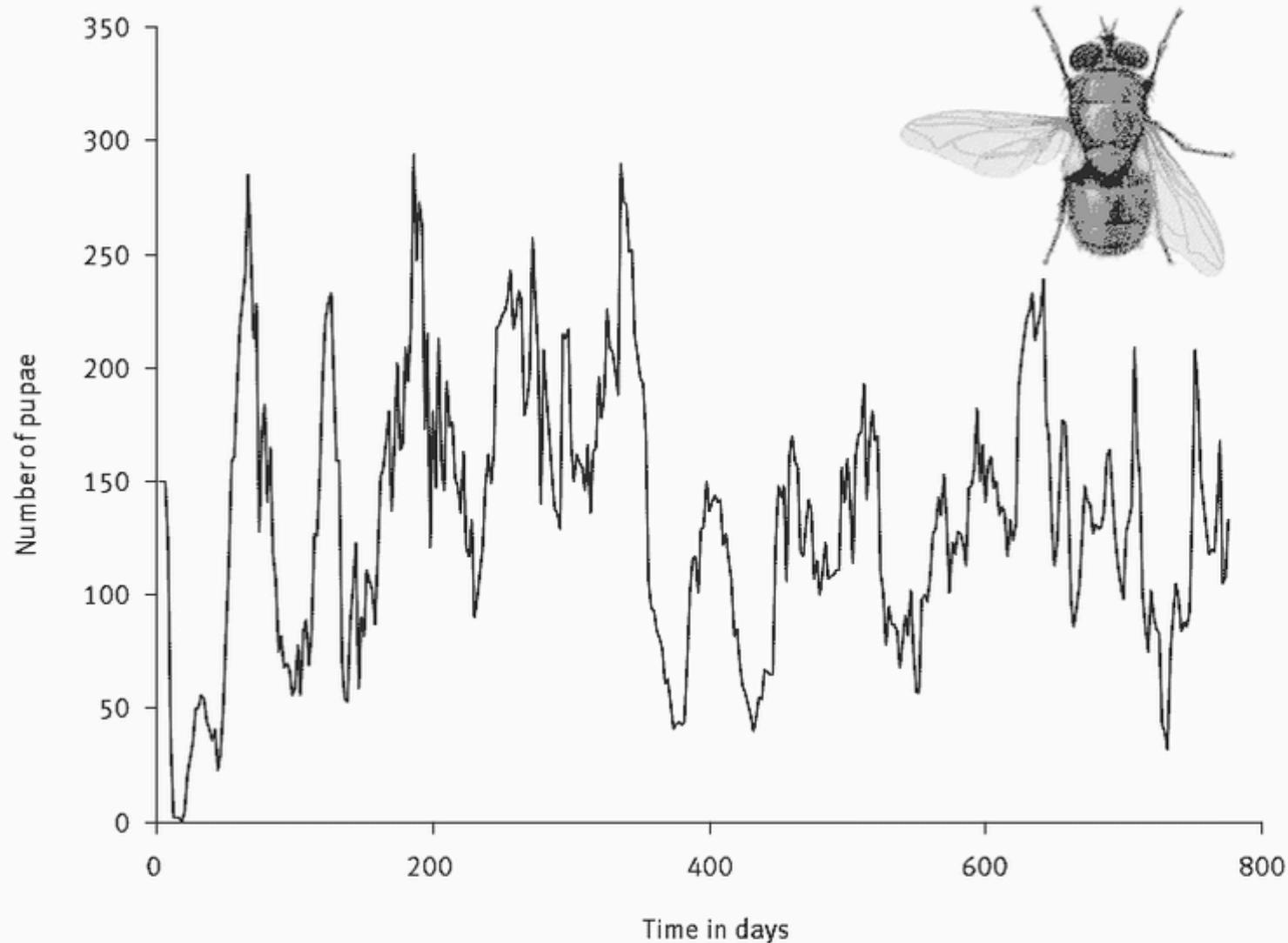
Initial population size  $N_0 = 1.01$



Ricker model:  $r = 3.5, K=20$



Photo credit: Fir0002/Flagstaffotos



**Figure 6.1** The number of pupae of the green bottle (sheep blowfly), in a laboratory population monitored every two days for two years. Data kindly made available to researchers by Robert Smith and colleagues (see <http://mcs.open.ac.uk/drm48/chaos/>).<sup>1</sup>



## Patterns of Dynamical Behaviour in Single-Species Populations

M. P. Hassell; J. H. Lawton; R. M. May

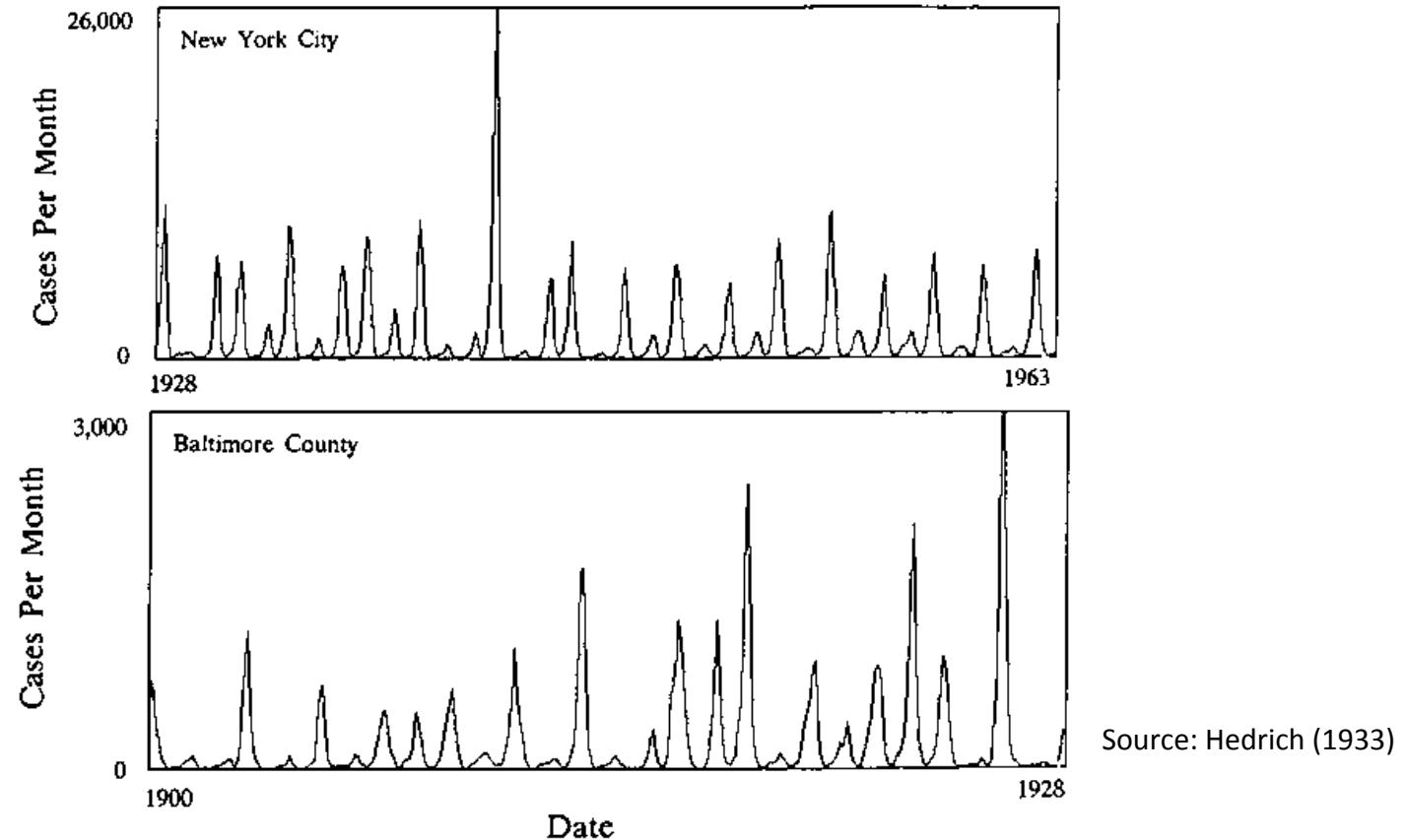
*The Journal of Animal Ecology*, Vol. 45, No. 2 (Jun., 1976), 471-486.

- 28 insect data sets
- Only the laboratory study of blowflies by Nicholson had parameters in the chaotic regime
- Could be a laboratory artifact: not subject to natural mortality from parasitic wasps



Photo credit: Andre Karwath

- 27 (Thomas et al. 1980) and 25 (Mueller and Ayala 1991) genetically distinct fruit fly populations
- No evidence of chaos



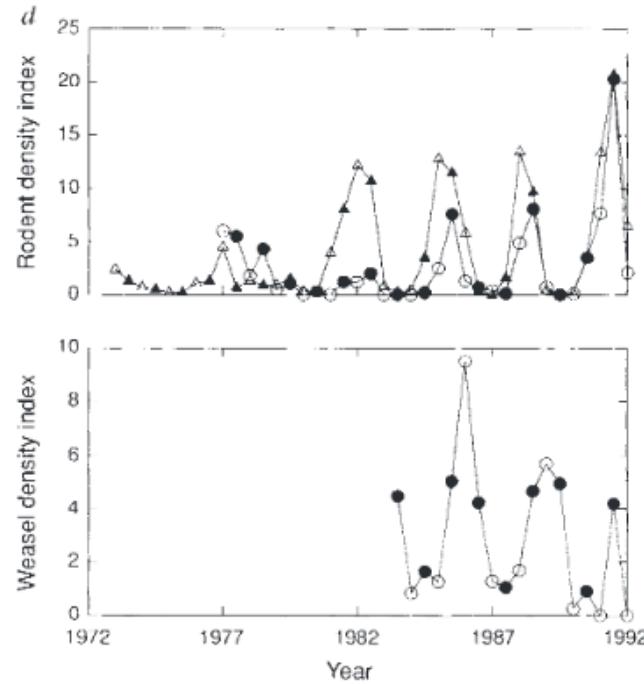
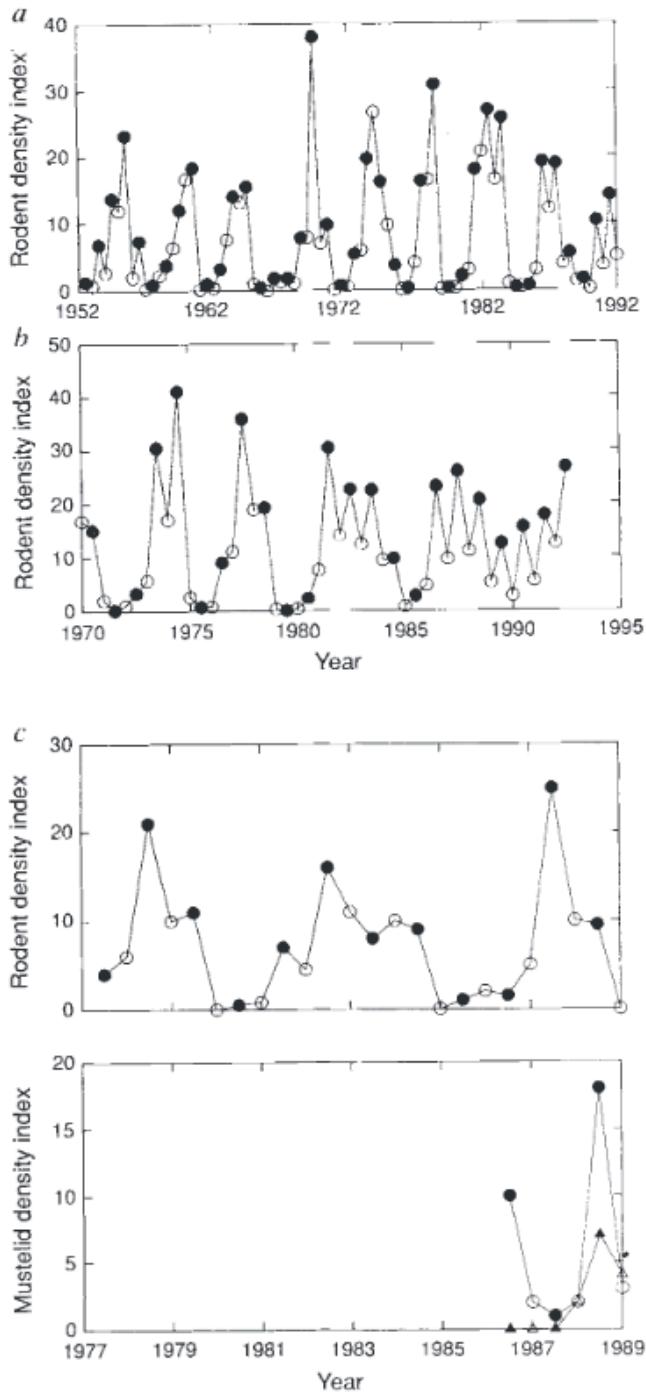
Source: Hedrich (1933)

- Measles in NYC and Baltimore, 1928-1963
- Analyses find the dynamics are chaotic
- Doubts: birth rates have changed over time, amount of seasonal forcing required to generate chaos more than observed



Photo credit: Fer boei

- *Microtus* voles in western Finland
- Time series shows ‘chaos superimposed’ on top of a more regular signal.



Since 1984, 3 yr cycles

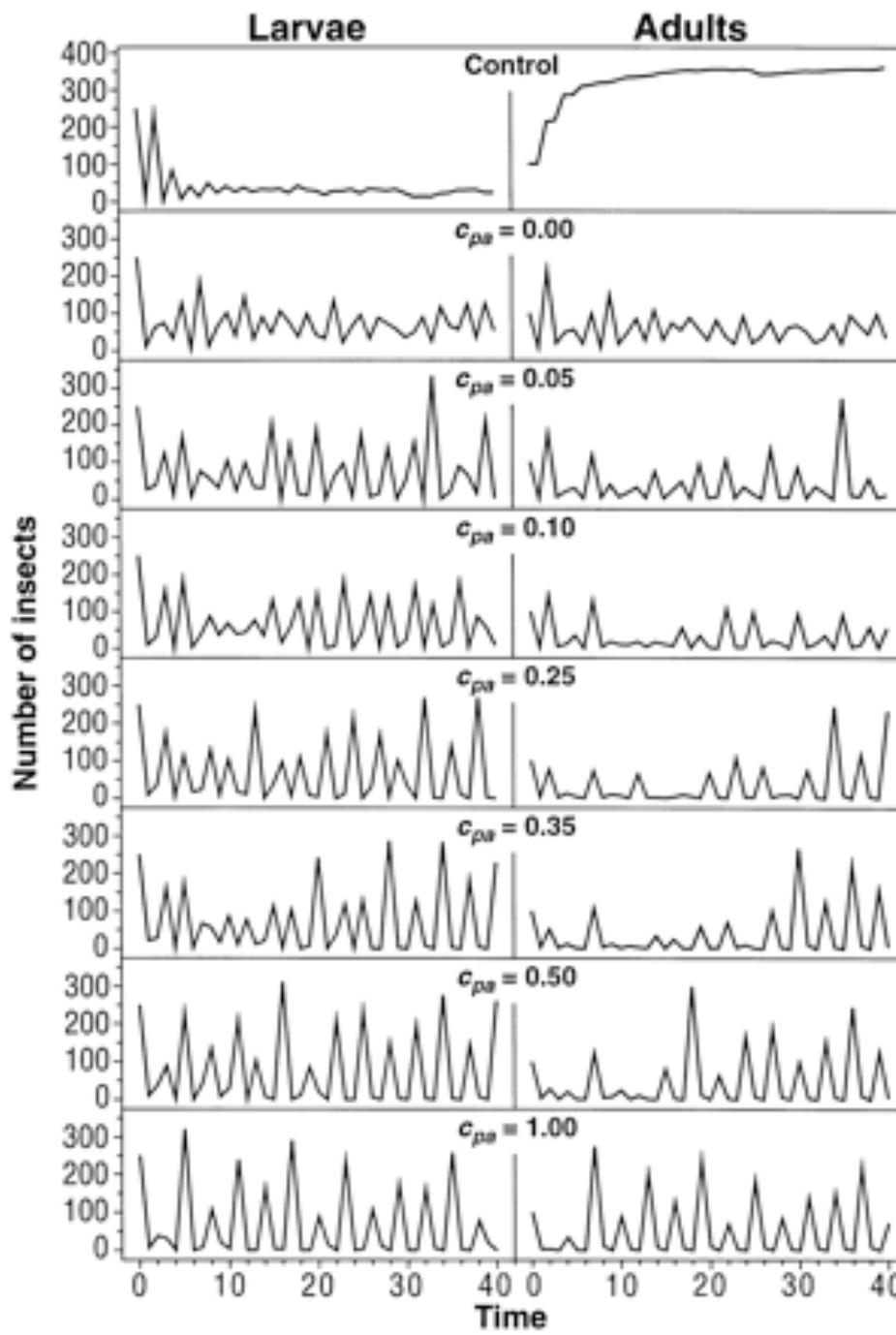
Multiannual cycles absent since 1980

FIG. 2 Four examples of observed long-term rodent dynamics. a, Kilpisjärvi, Finnish Lapland, pooled density of 5 vole species<sup>30,31</sup> (H.H., unpublished results); b, Pallasjärvi, Finnish Lapland, pooled density of 5 vole species in old taiga forest (H.H., unpublished results); c, Iesjavri basin, Norwegian Lapland; upper panel, pooled data for 3 vole species; lower panel, the least weasel and the stoat<sup>9</sup>; d, Alajoki western Finland; upper panel, *Microtus* densities at 2 study sites separated by 14 km; lower panel, the least weasel densities<sup>8,26</sup>. Open symbols give spring densities, filled symbols autumn densities.



## Flour beetles (*Tribolium castaneum*)

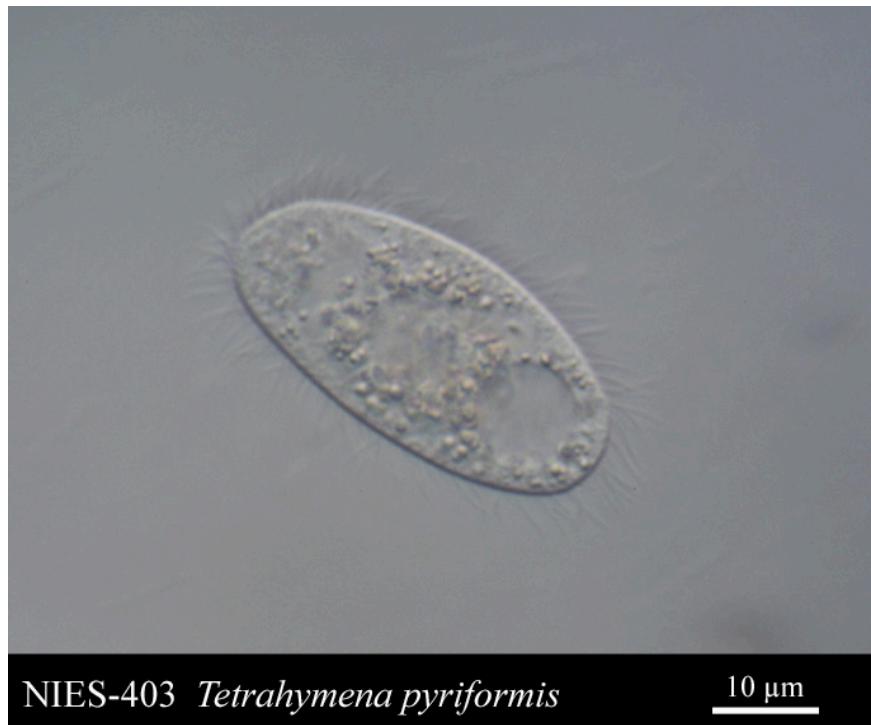
- Artificially manipulated adult mortality and the pupae to adult recruitment rate to generate chaos
- Criticism: forced the system to match the model not other way around



Equilibrium

chaos

period-3 cycle

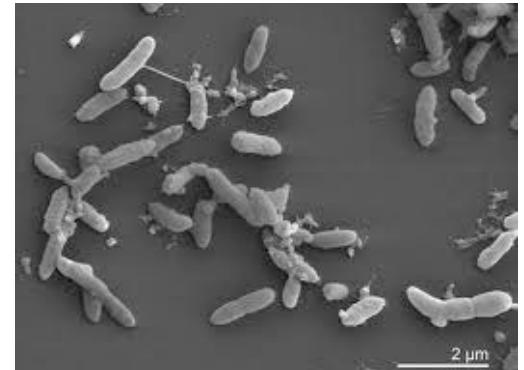


NIES-403 *Tetrahymena pyriformis*

source: [www8.umoncton.ca](http://www8.umoncton.ca)

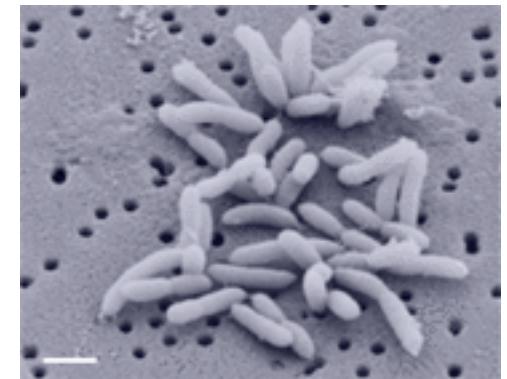
10 μm

**Pedobacter**



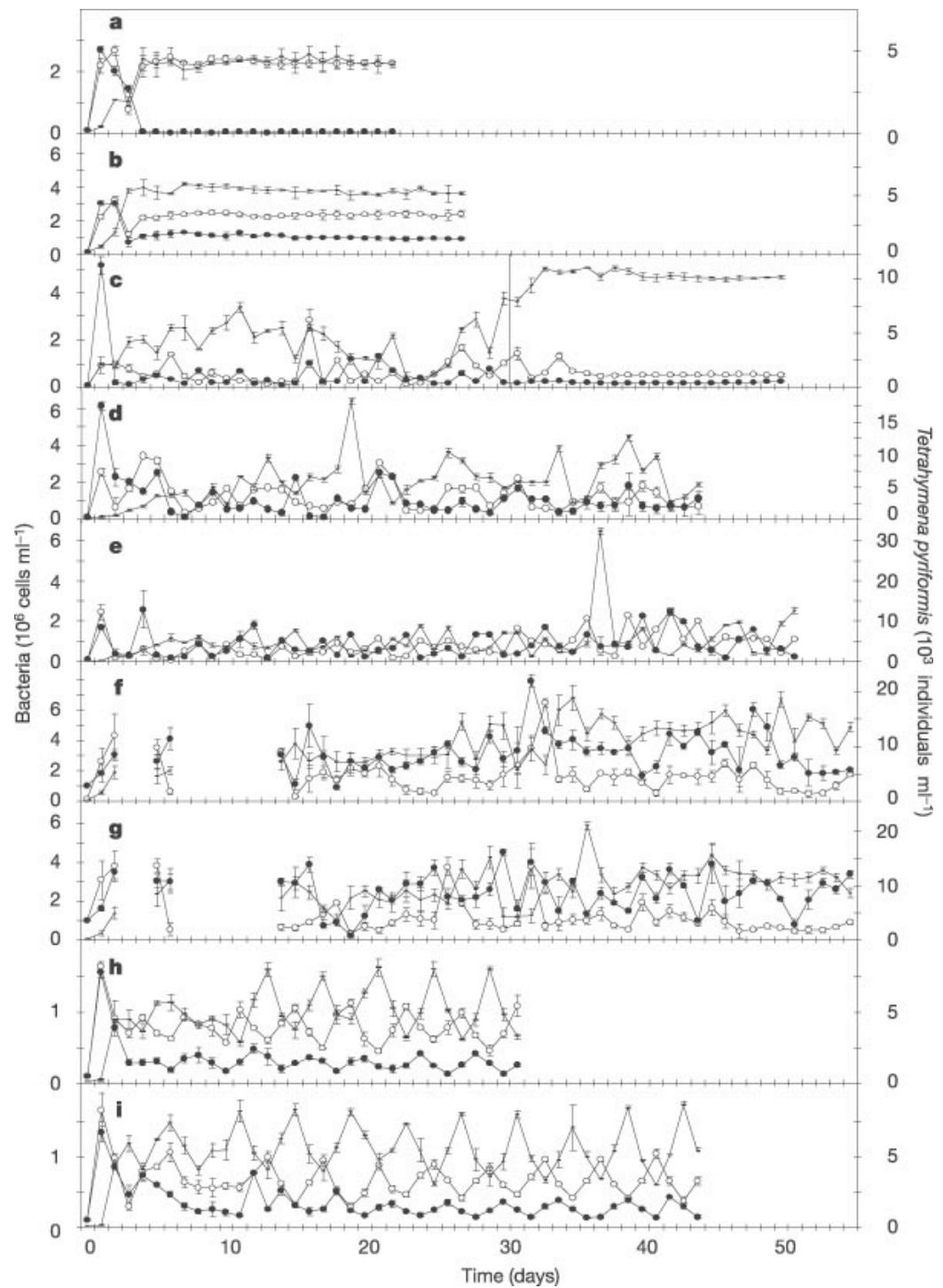
Source: <http://bacmap.wishartlab.com/organisms/937>

**Brevundimonas**



Source: [https://microbewiki.kenyon.edu/index.php/Brevundimonas\\_diminuta](https://microbewiki.kenyon.edu/index.php/Brevundimonas_diminuta)

- Laboratory experiments with bacteria-eating ciliate predator and two species of bacteria
- Evidence of chaotic dynamics



Source: Becks et al. 2005. Nature.

## Summary

- “we cannot rule out the possibility ... [of chaos in nature] ...but the case is looking increasingly shaky, at least for multicellular organisms.
- Data sets are short term and noisy.

