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:

$$N(t) = \frac{KN_0e^{rt}}{K + N_0(e^{rt} - 1)}$$

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

DensityDependentGrowth.R

Source on Save Run Source

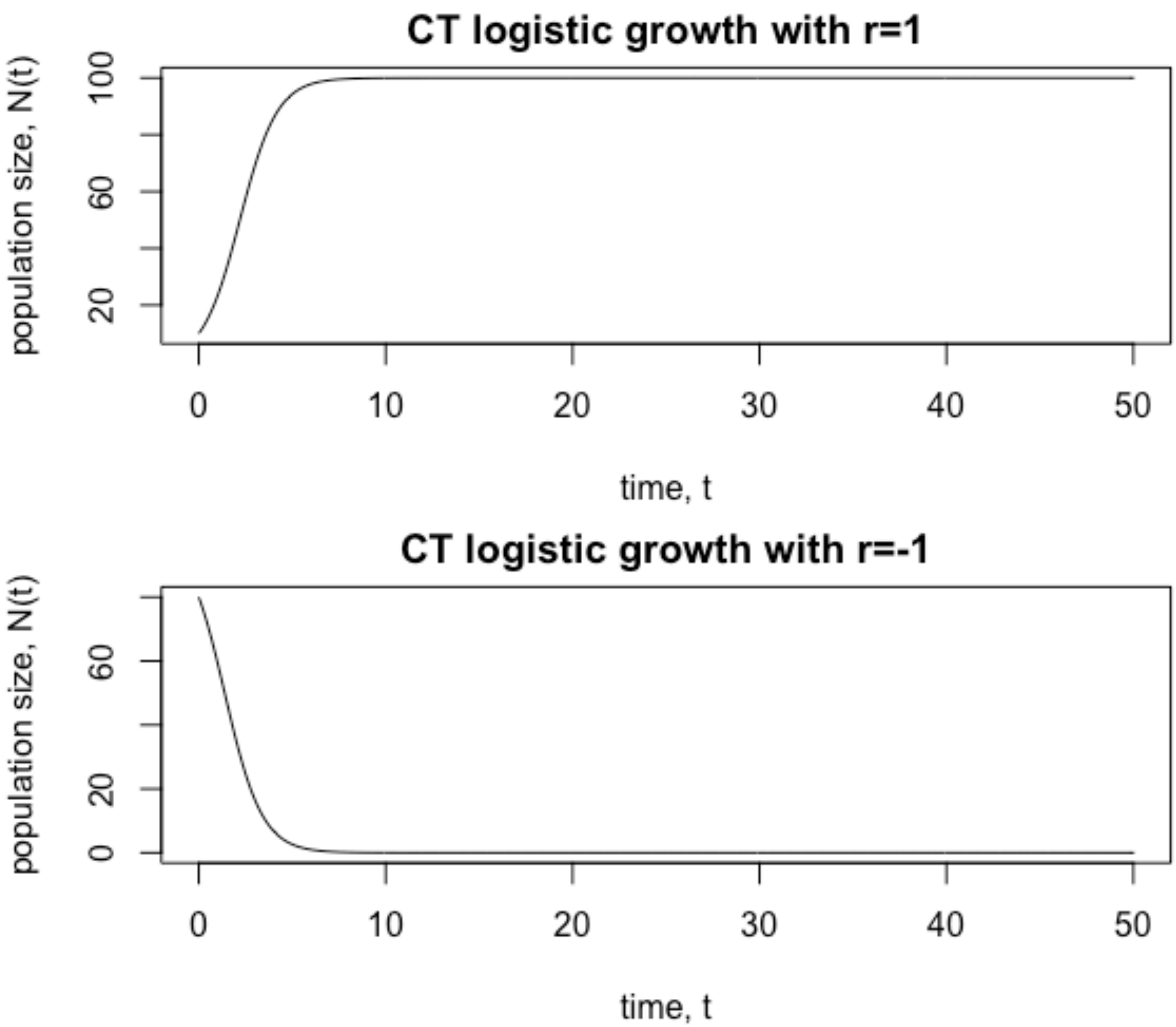
```r
# SOLVING MODELS FOR DENSITY-DEPENDENT POPULATION GROWTH
#----------
# Models:
# 1) Continuous time logistic growth
# 2) Discrete time logistic map
# 3) Altervative version of the discrete time logistic map
# 4) Ricker model (discrete time)
# 5) Beverton-Holt model (discrete time)

# Remove all objects - always start with this
rm(list=ls())

# load the package to numerically solve the continuous time
# model
require(deSolve)

```

Logistic growth (continuous time)



Equilibrium points

- Values of $\mathrm{N}(\mathrm{t})$ such that $\frac{dN(t)}{dt} = 0$

- Equilbria can be unstable

- Stability of equlibrium can be determined by a line-arrow diagram

Logistic growth (continuous time)

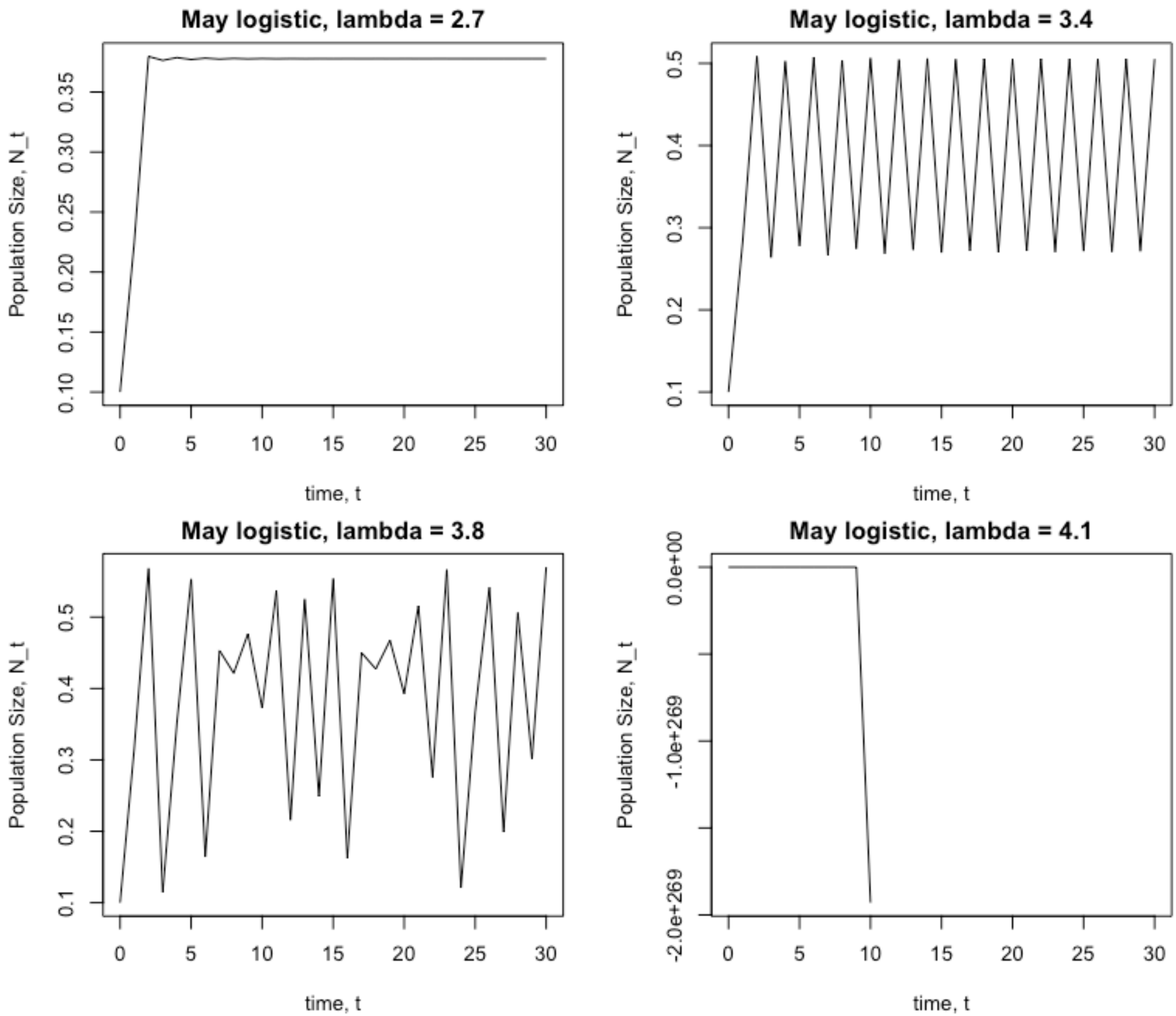
- $N(t) = 0$ is stable when $r < 0$
- $N(t) = K$ is stable when $r > 0$

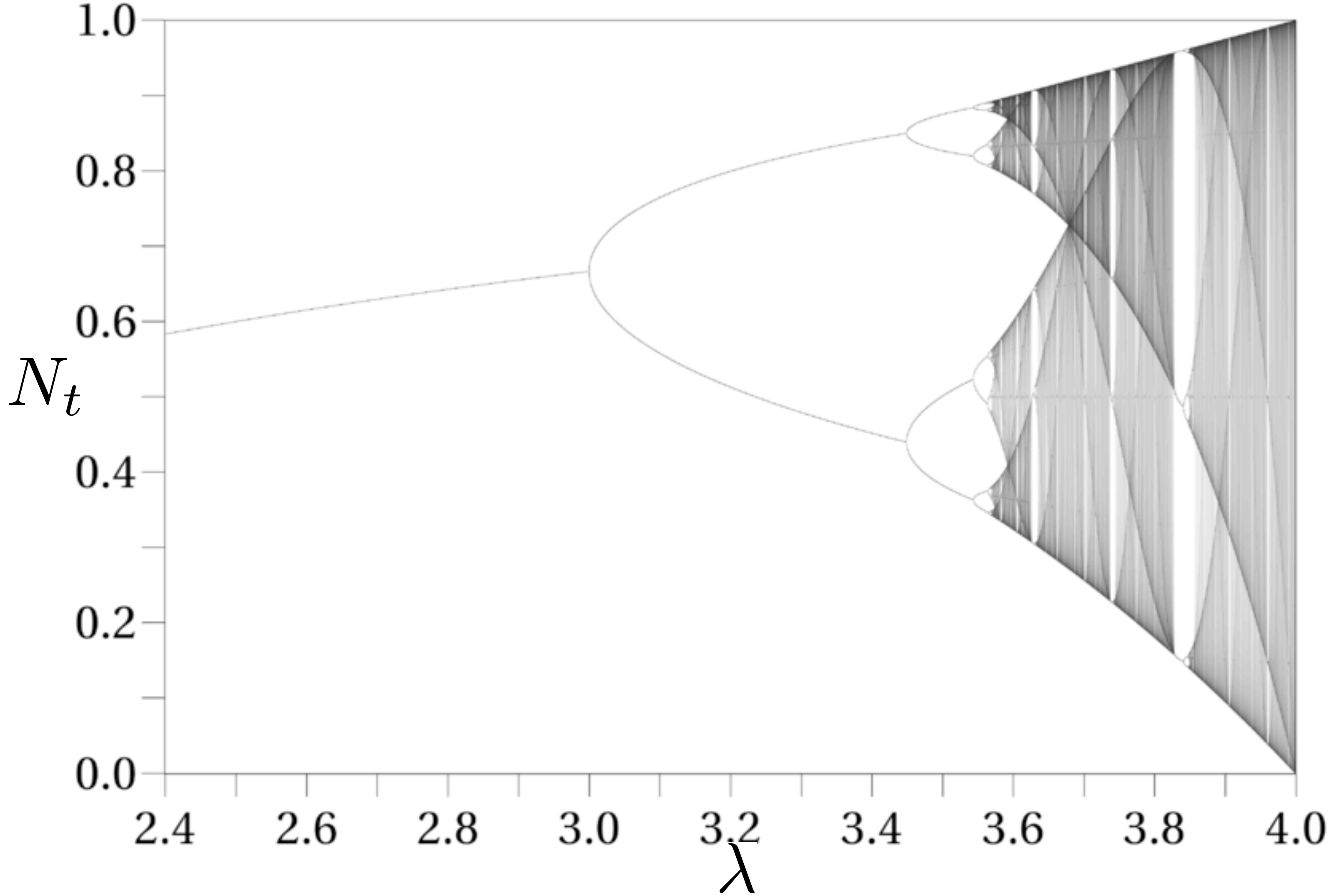
Logistic growth (discrete time)

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

- 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 λ=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
Population Size, N_t
time, t
May logistic, lambda = 3.4
Population Size, N_t
time, t
May logistic, lambda = 3.8
Population Size, N_t
time, t
May logistic, lambda = 4.1
Population Size, N_t
time, t
0.0e+00
-1.0e+269
-2.0e+269



1.0
0.8
0.6
0.4
0.2
0.0
N_t
2.4
2.6
2.8
3.0
3.2
3.4
3.6
3.8
4.0
λ

Logistic growth (discrete time)

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

- 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,

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

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

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

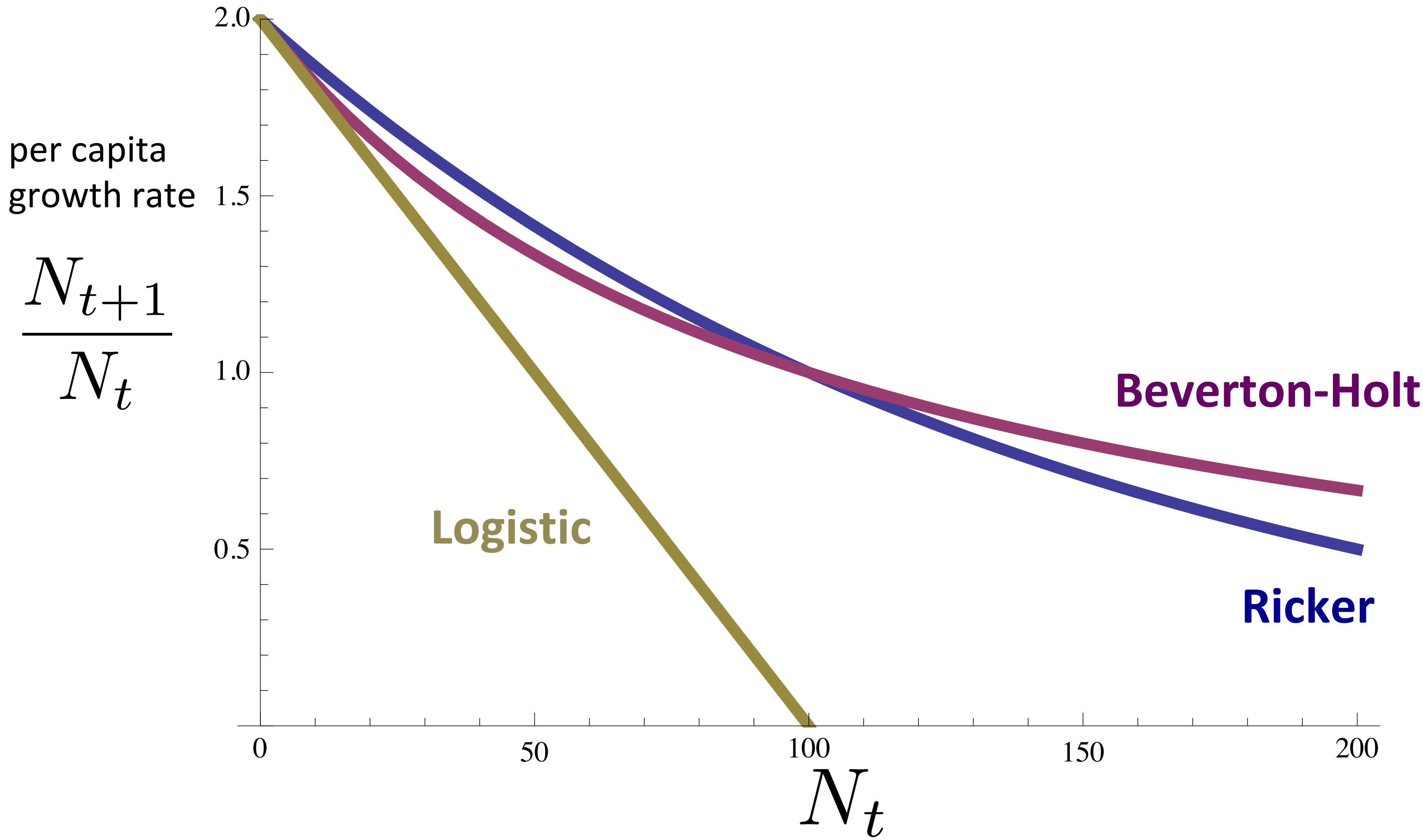
The Ricker model has a similar overall form, although its formulation is exponential, namely,

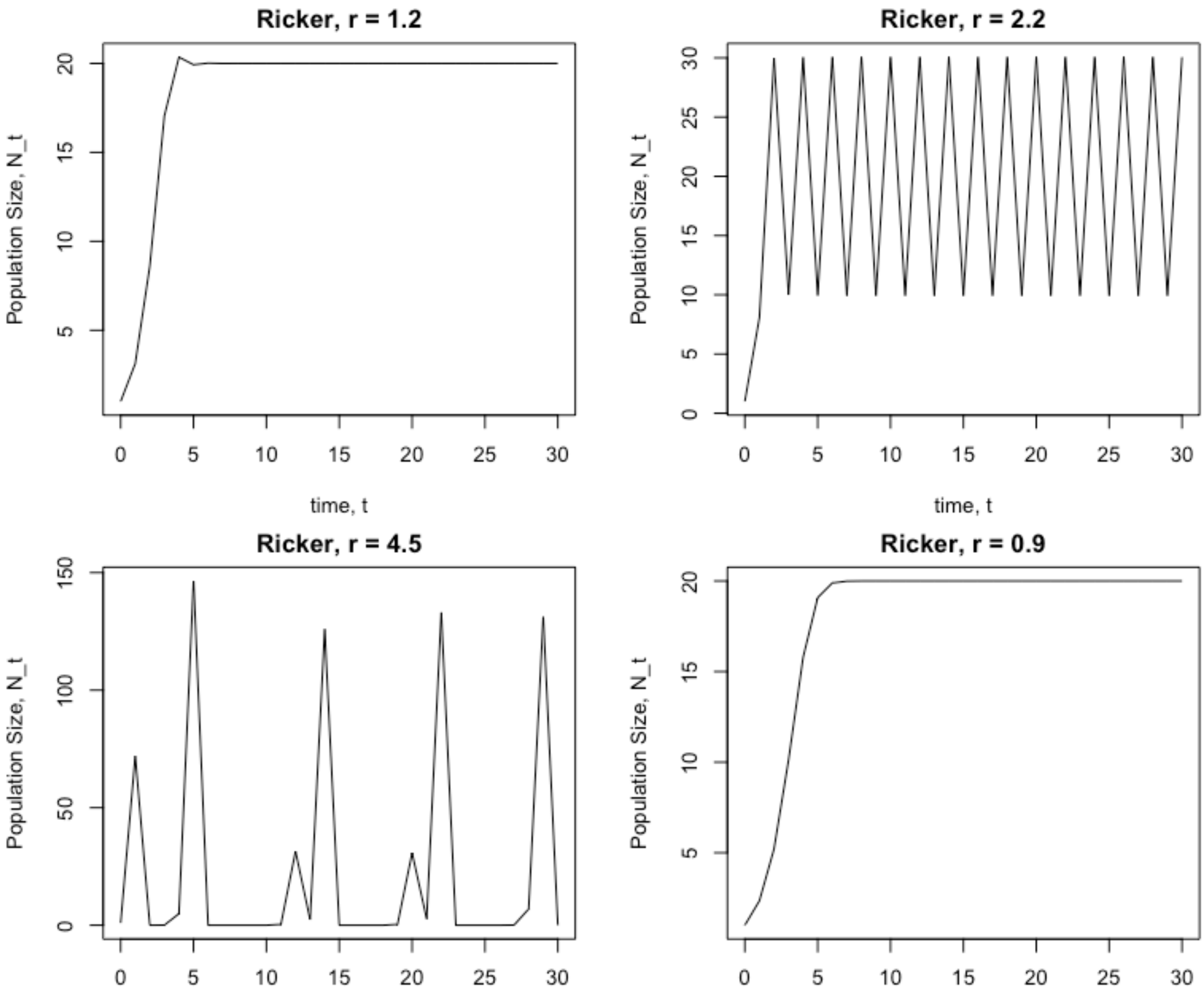
$$N_{t+1} = N_t e^{r(1 - bN_t)}. \tag{30}$$

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-

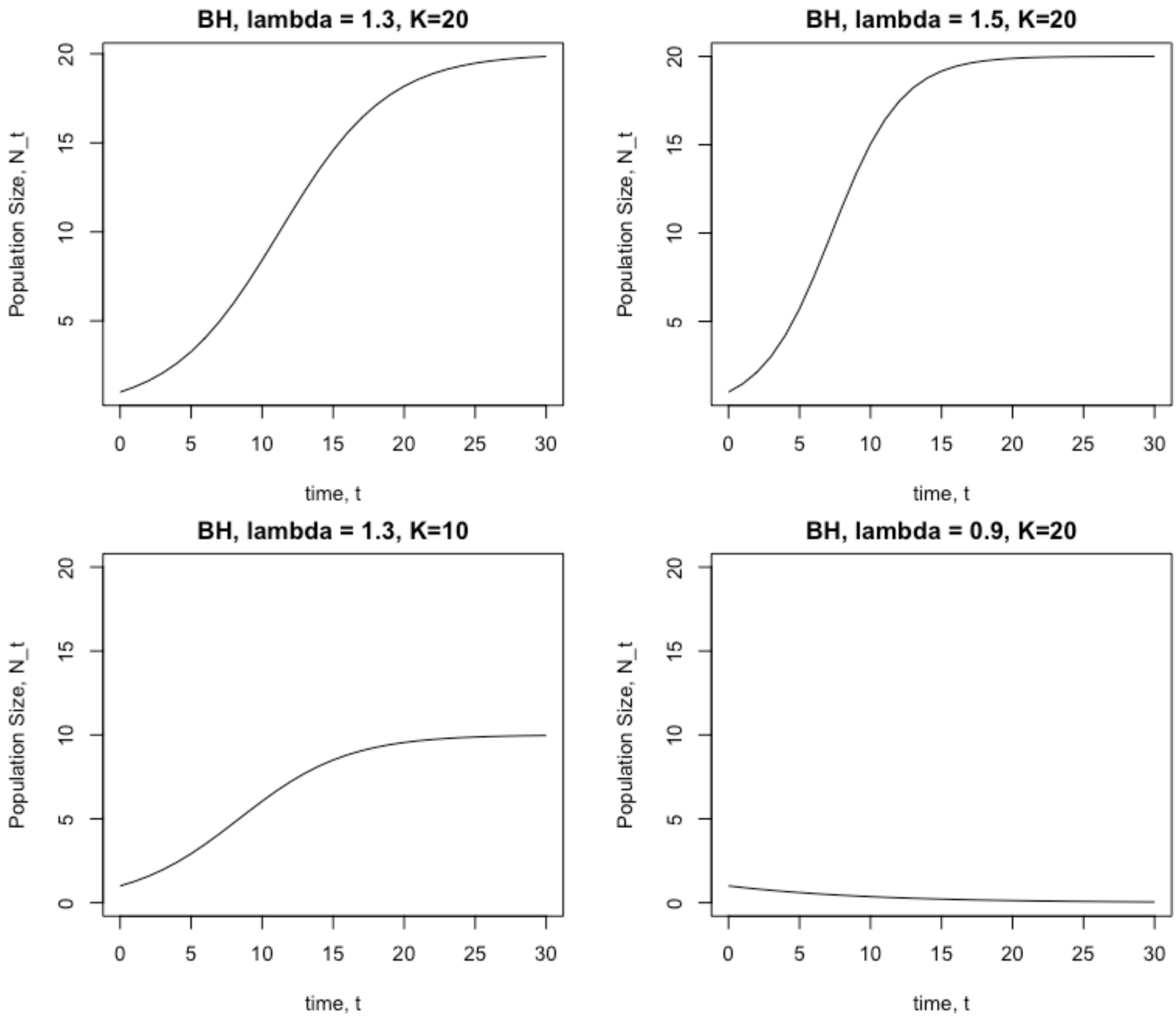
Vandermeer and Gordon p29

Discrete time models of density-dependent population growth





Ricker, r = 1.2
Ricker, r = 2.2
Ricker, r = 4.5
Ricker, r = 0.9
Population Size, N_t
time, t



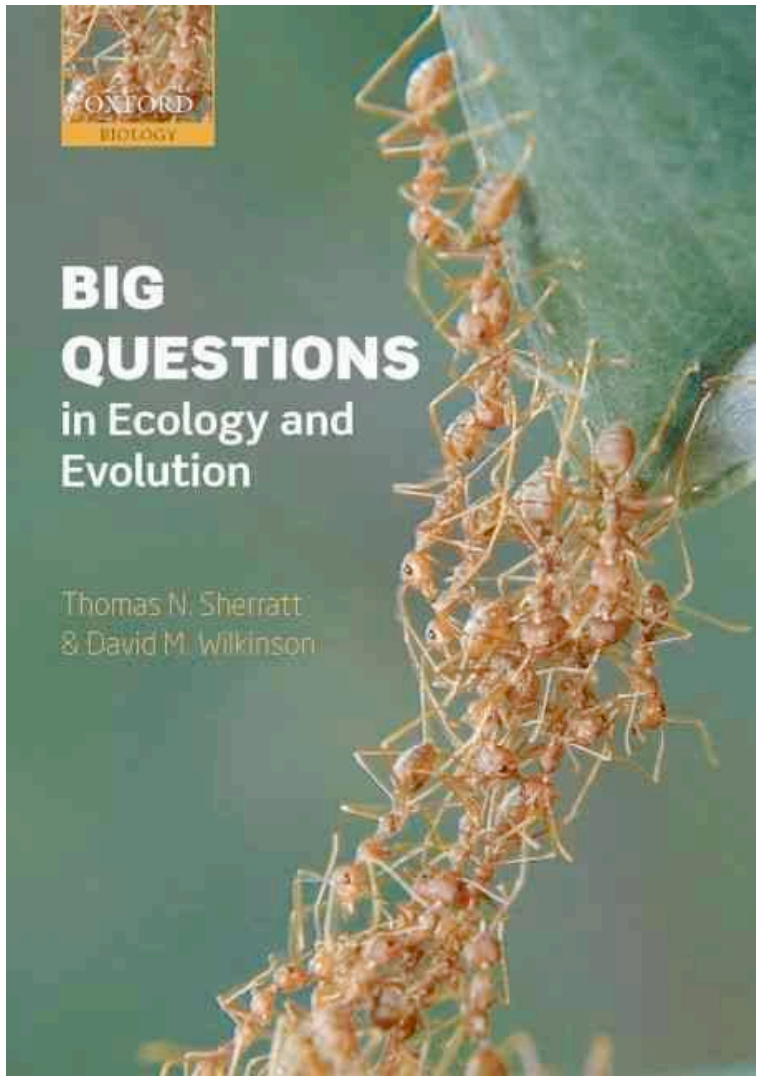
BH, lambda = 1.3, K=20
BH, lambda = 1.5, K=20
BH, lambda = 1.3, K=10
BH, lambda = 0.9, K=20
Population Size, N_t
time, t
0
5
10
15
20
25
30

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

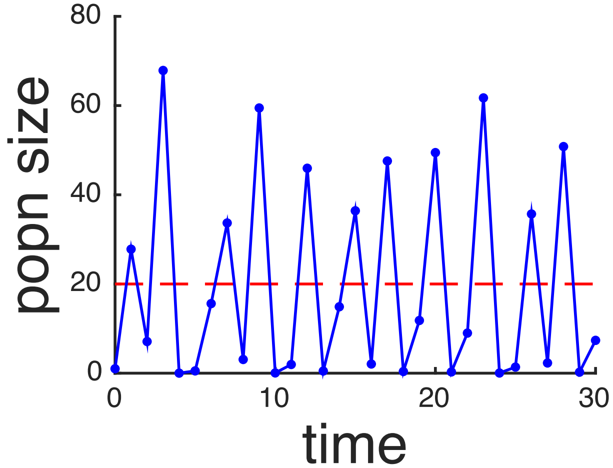
a. Equilibrium at 0; b. Equilibrium at K;

c. Periodic cycles; d. Chaos

Do biological populations exhibit chaotic dynamics?

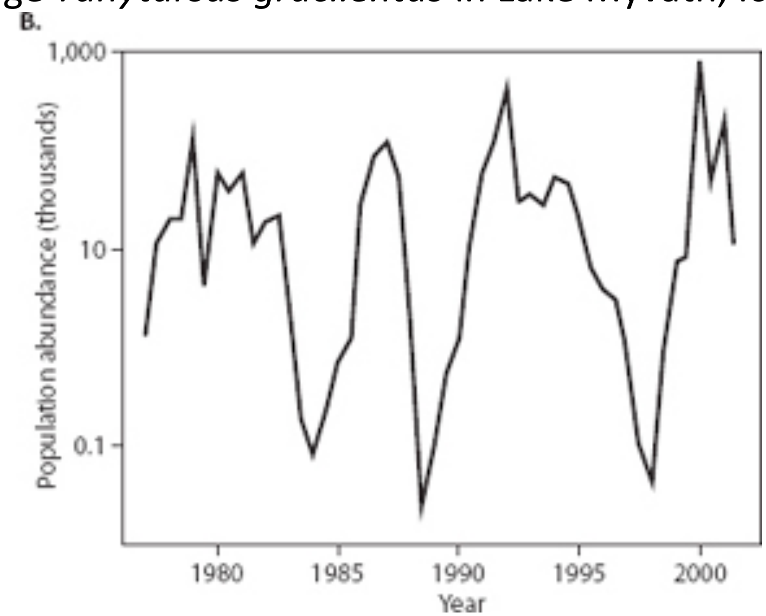


How to identify chaos?



The midge *Tanytarsus gracilentus* in Lake Myvatn, Iceland

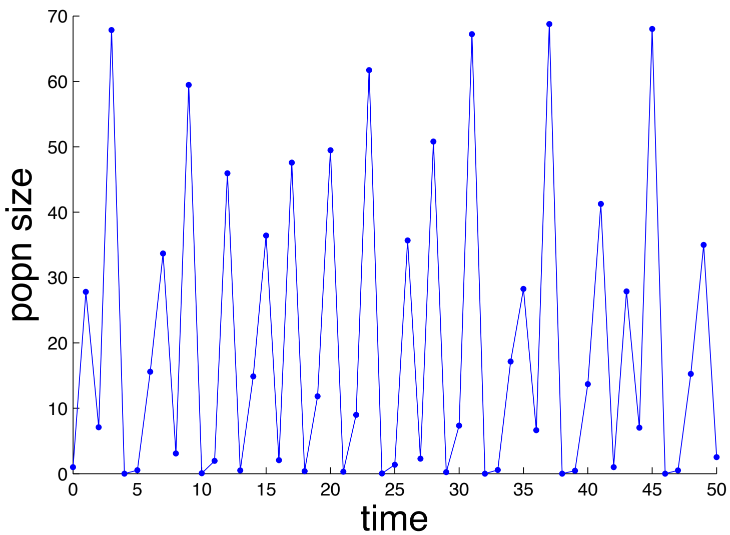
Photo credit: Kenneth Chang



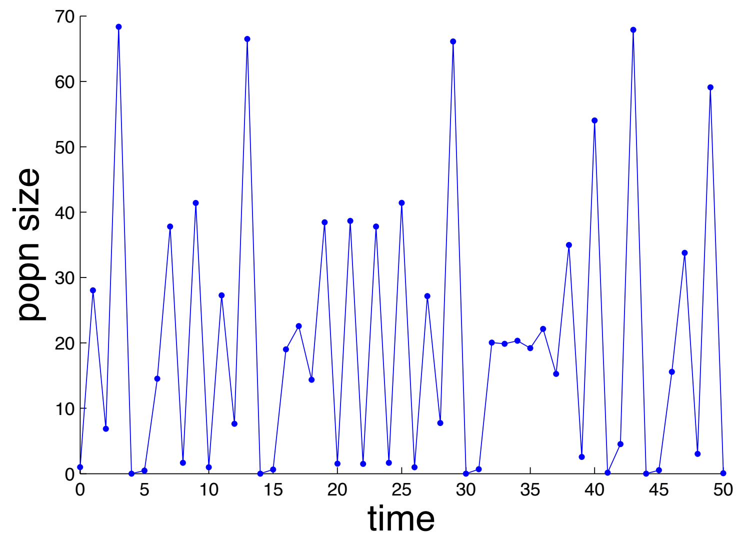
Definition of chaos

- ‘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

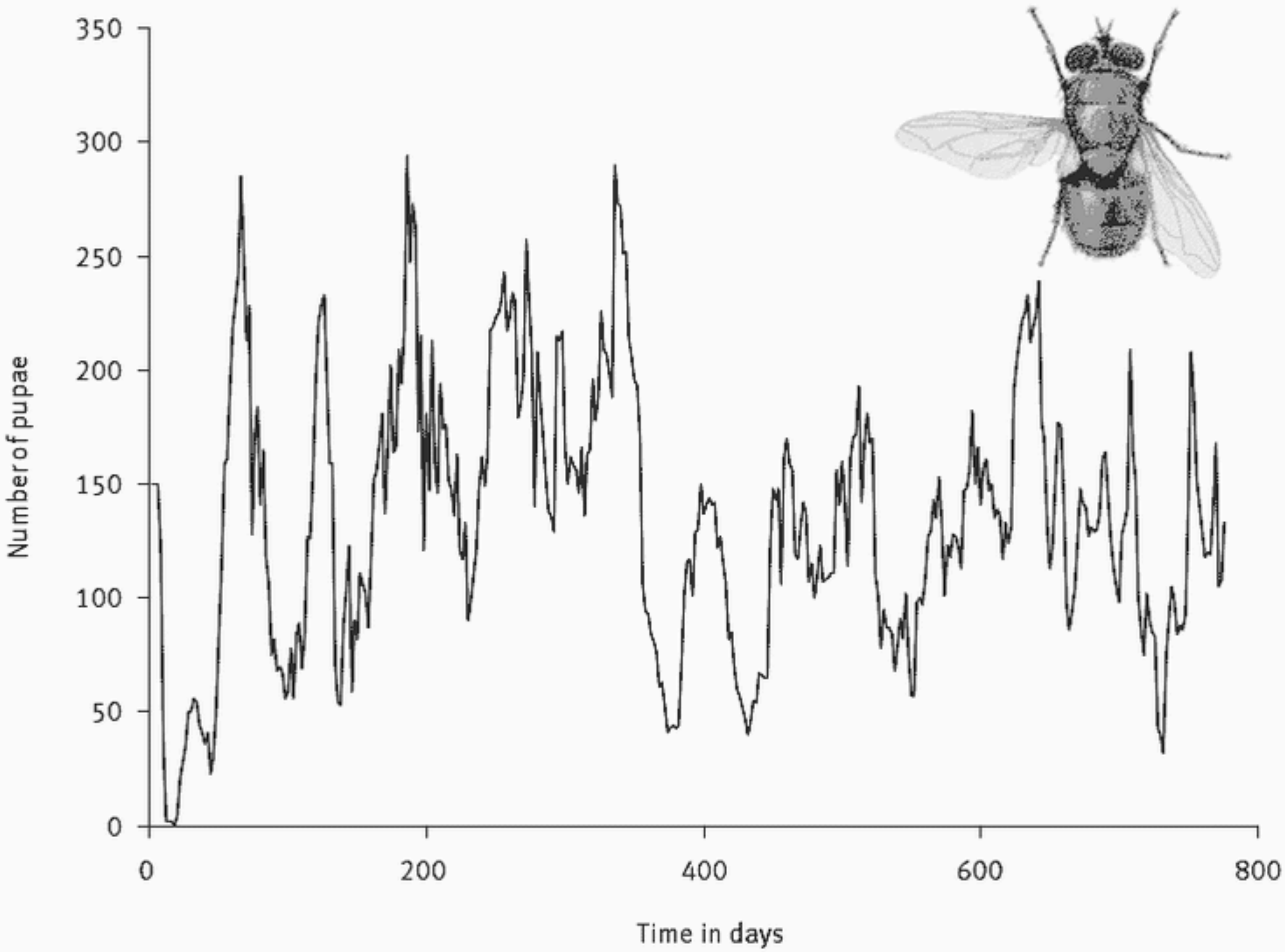


Figure 6.1 The number of pupae of the green bottle (sheep blowfly), in a laboratory population monitored every two days for two years. Data kindly made available to researchers by Robert Smith and colleagues (see http://mcs.open.ac.uk/drm48/chaos/).[1]

Patterns of Dynamical Behaviour in Single-Species Populations

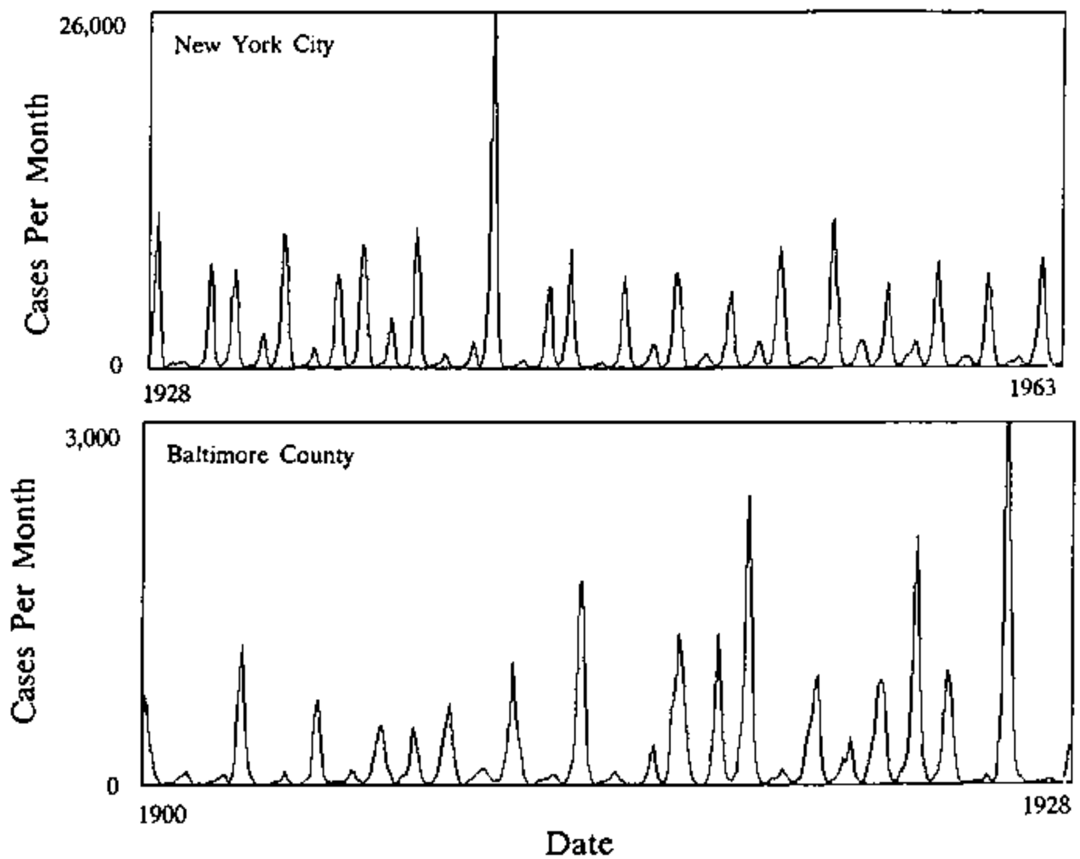
M. P. Hassell; J. H. Lawton; R. M. May

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

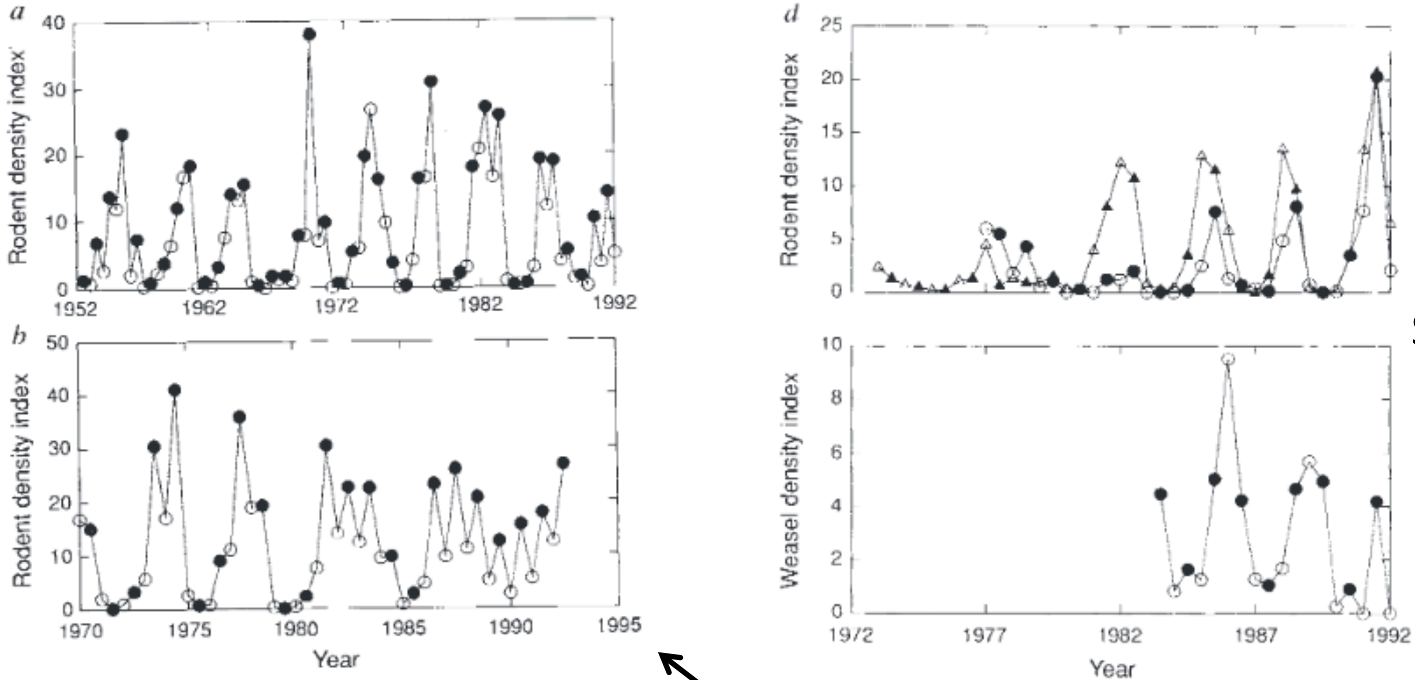


Source: Hedrich (1933)

- 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

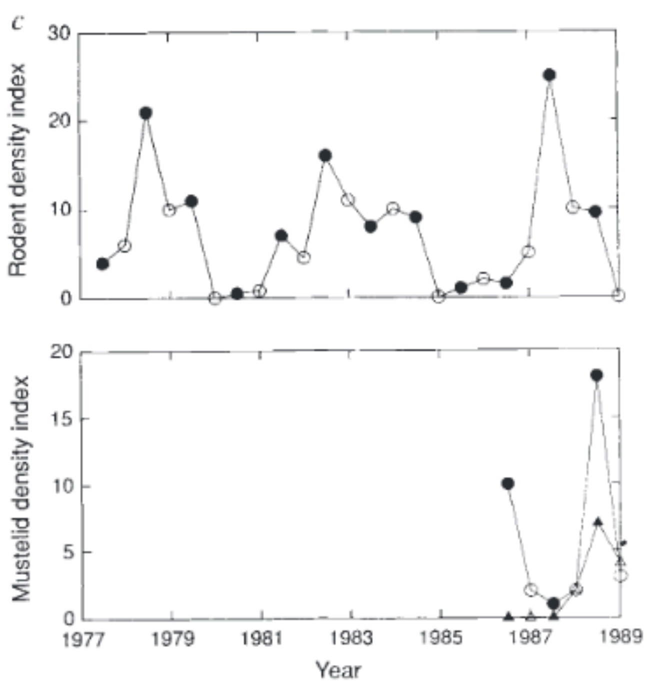
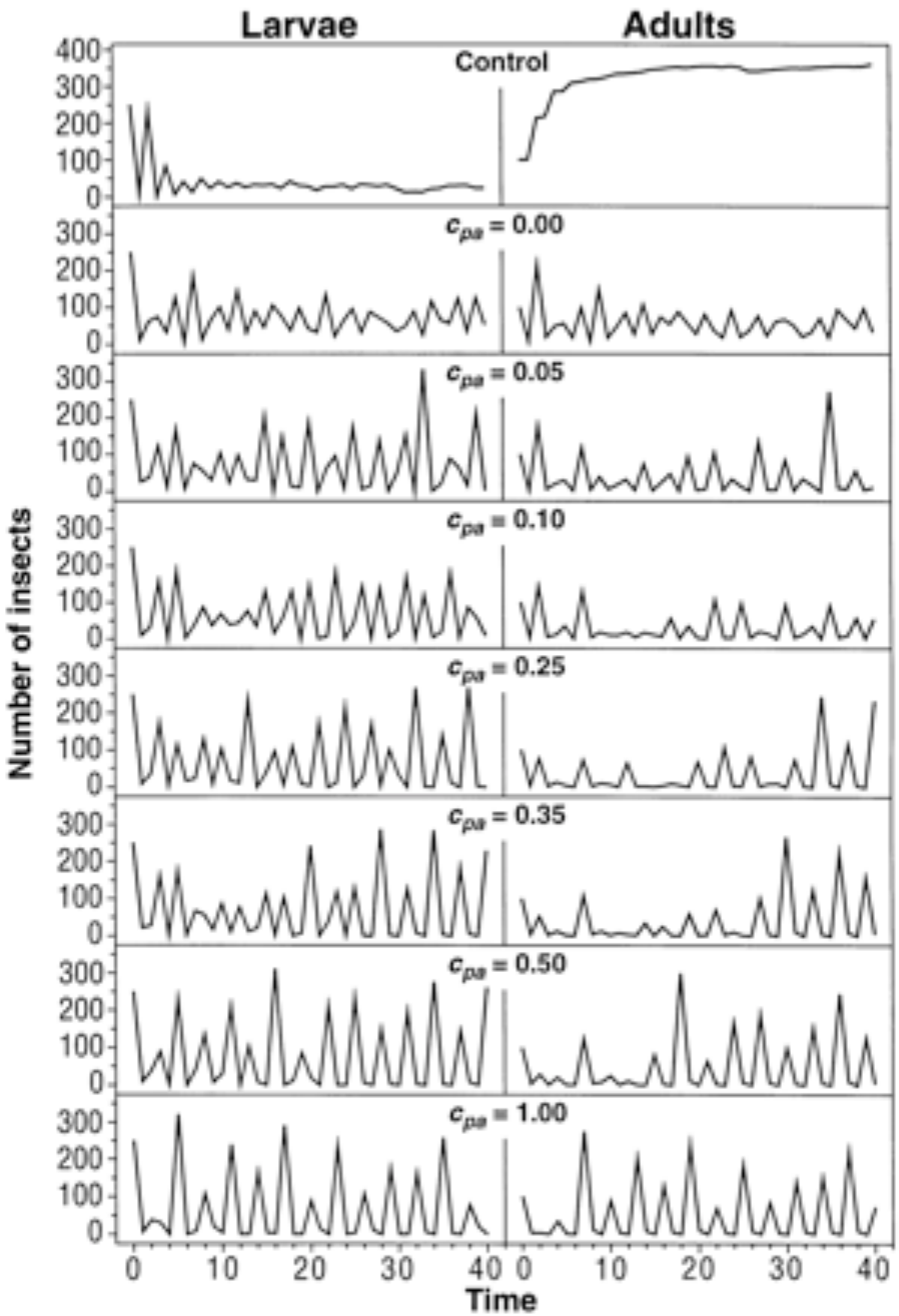


FIG. 2 Four examples of observed long-term rodent dynamics. *a*, Kilpisjärvi, Finnish Lapland, pooled density of 5 vole species[30,31] (H.H., unpublished results); *b*, Pallasjärvi, Finnish Lapland, pooled density of 5 vole species in old taiga forest (H.H., unpublished results); *c*, Iesjavri basin,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

Hanski et al. 1993 Nature

<u>Flour beetles (*Tribolium castaneum*)</u>

- 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

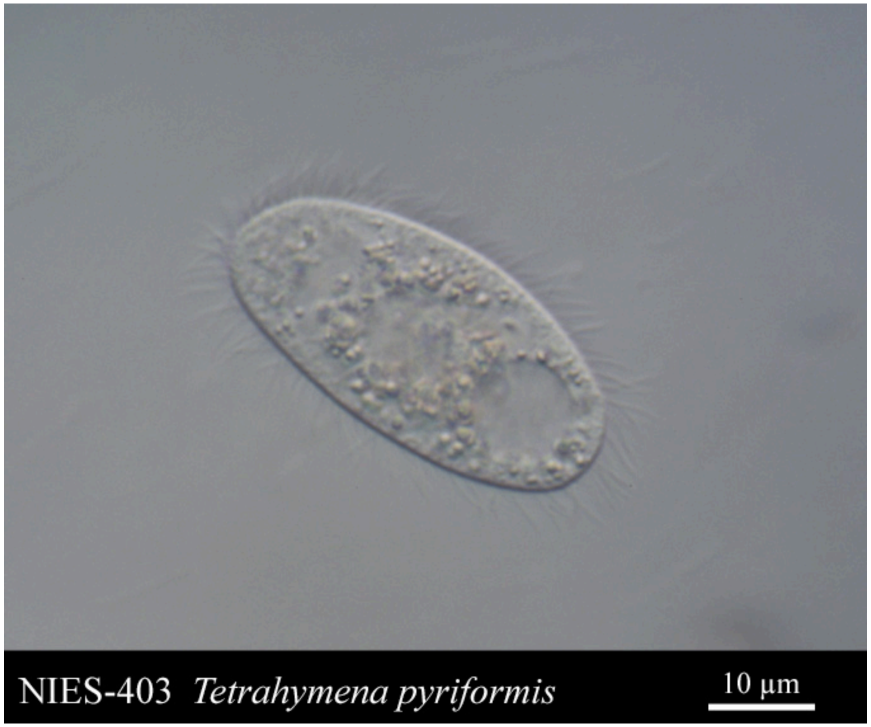


Equilibrium

chaos

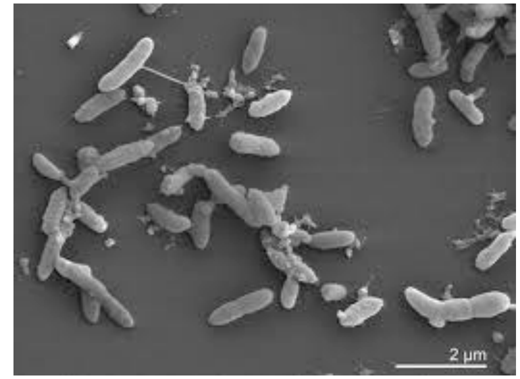
period-3 cycle

Costantino et al. 1997



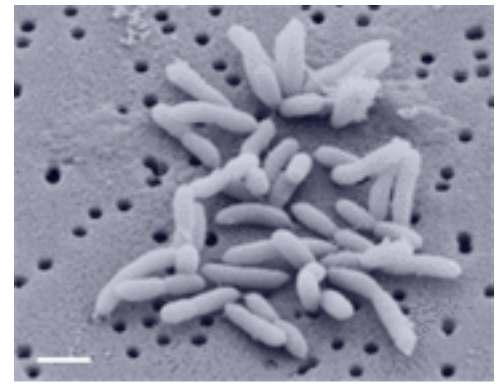
source: www8.umoncton.ca

Pedobacter



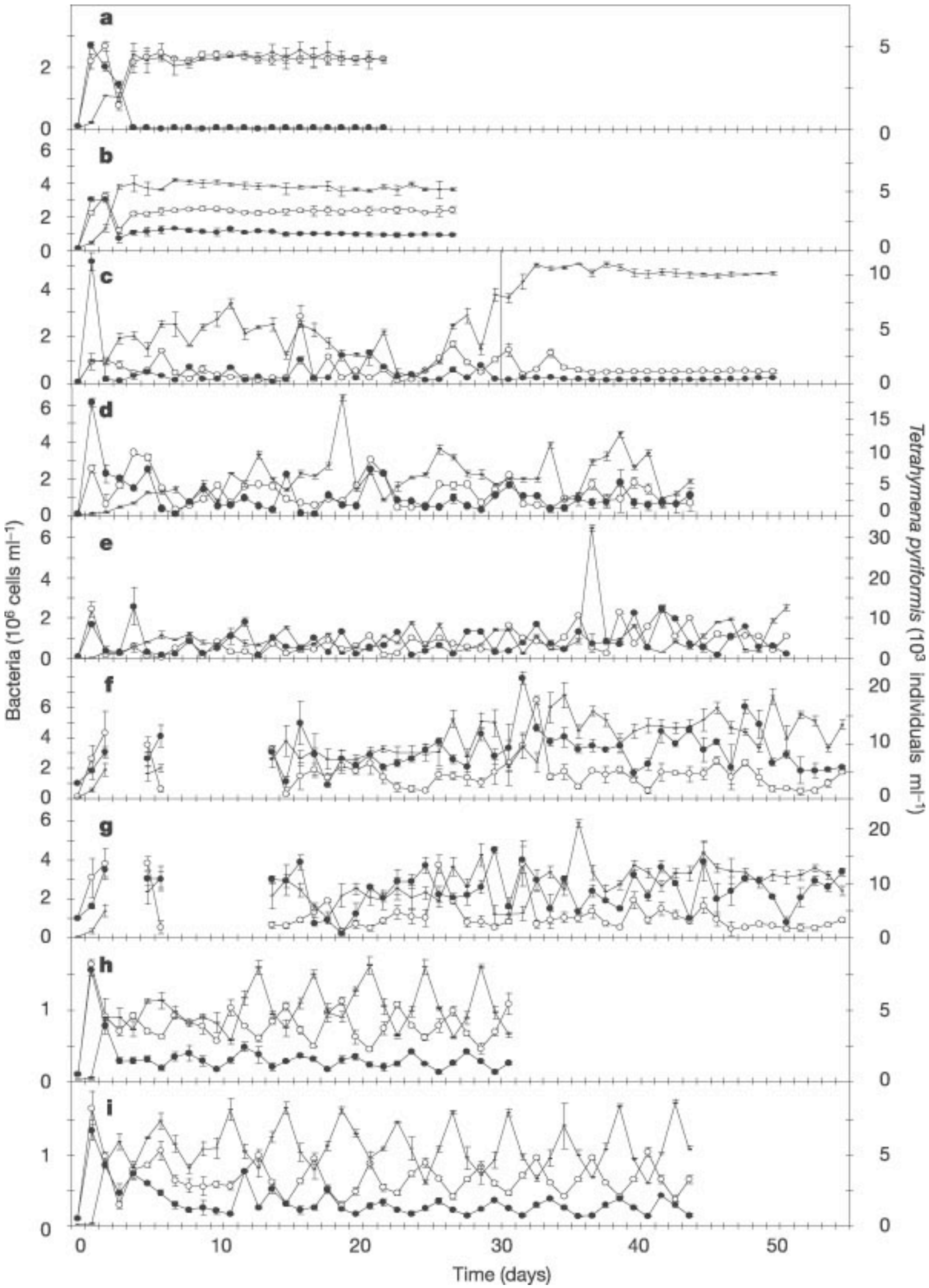
Source: http://bacmap.wishartlab.com/organisms/937

Brevundimonas



Source: 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.