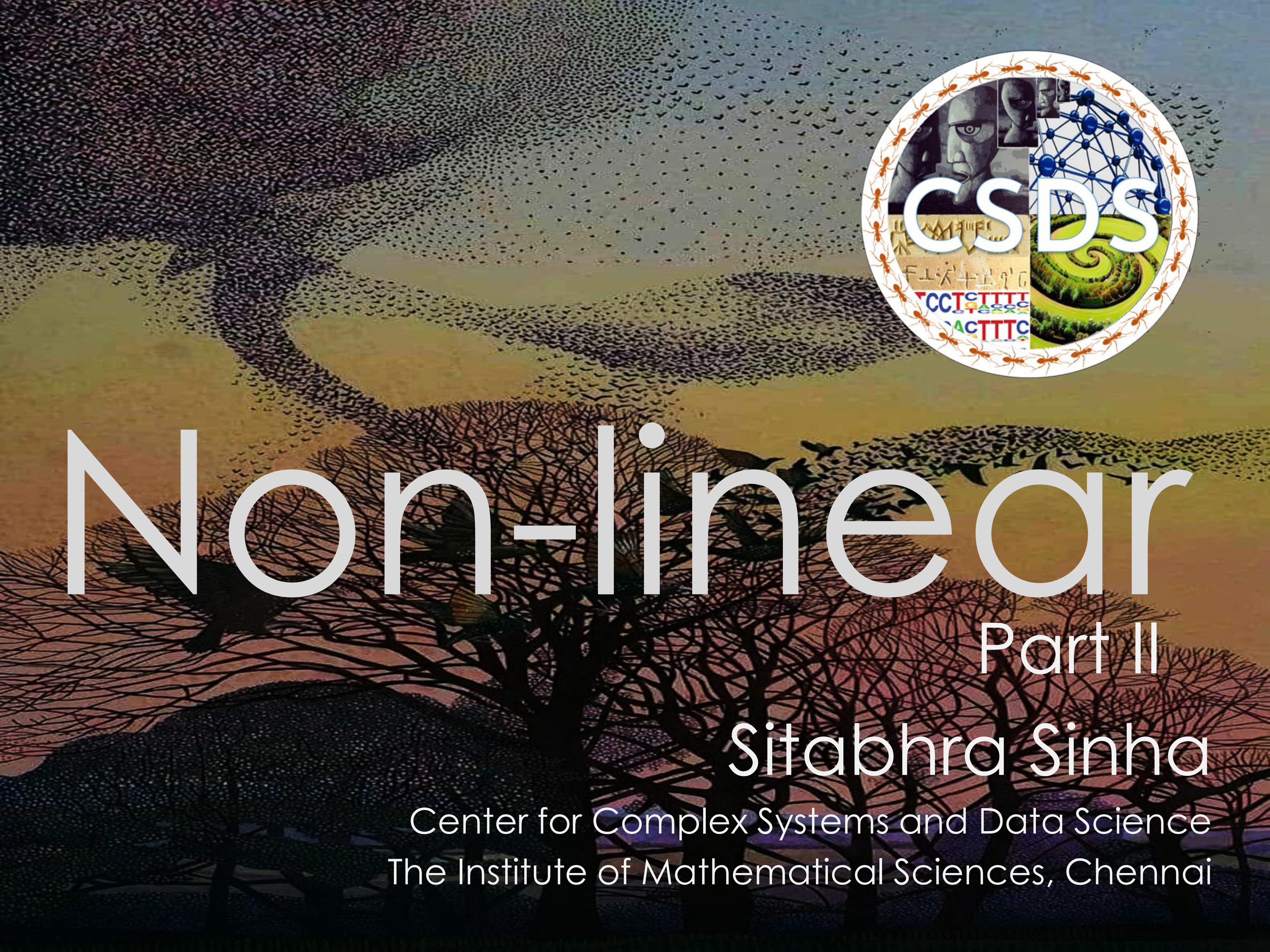


Non-linear

Part II

Sitabhra Sinha

Center for Complex Systems and Data Science
The Institute of Mathematical Sciences, Chennai

Laura & Petrarch's love was unconsummated…

… but the reason evolution came up with this complex emotion is so that…

Organisms can breed & population increases

Quantifying population growth

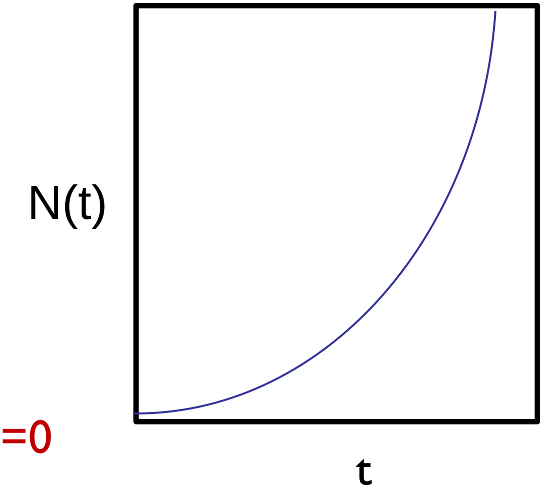
The simplest model for the growth of a population of organisms is

$dN/dt = r N$

$N(t)$: population at time t
r (>0) : growth rate

How will the population evolve with time ?

$N(t) = N(0) \exp(r t)$, where $N(0)$ is population at $t=0$



Bounded growth → Logistic growth eqn

Exponential growth cannot continue indefinitely.
To model the effects of **overcrowding** and **limited resources**,
we can assume that
the per capita growth rate $(dN/dt)/N$ decreases when N becomes sufficiently large

For small N, the growth rate equals the max rate r (where there is no limitation of resources/intra-species competition).

However, for populations larger than the **carrying capacity** K of the environment the growth rate becomes negative:
death rate > birth rate.

A simple choice for the functional relation between the per capita growth rate and N is a linear form:

$r \to r\,[(K - N)/K]$

which yields the logistic equation

$dN/dt = r\,N\,[1-(N/K)]$

Pierre Verhulst
1804 -1849

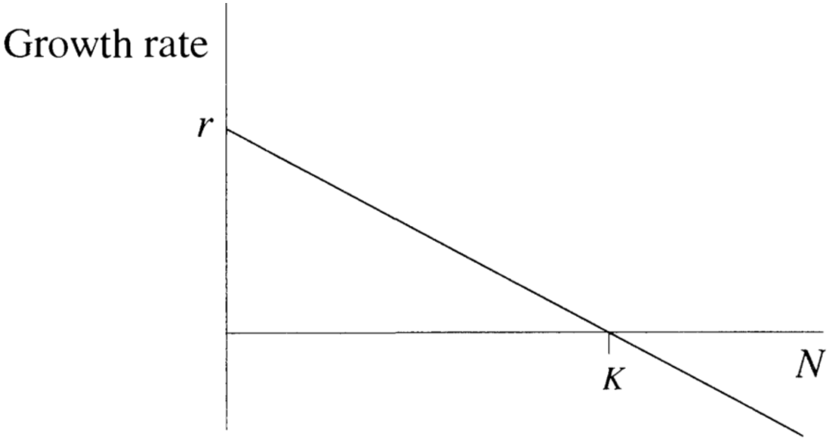
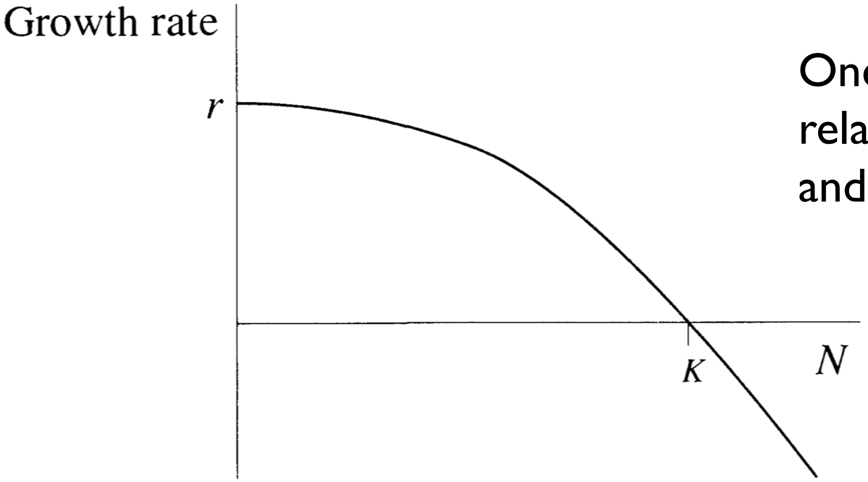


Image: Strogatz, *Nonlinear Dynamics and Chaos*

Alternative descriptions of bounded growth



One can make other choices for the functional relation between the per capita growth rate and N

BENJAMIN GOMPERTZ

1779-1865

If per capita growth rate = $a \log (K / N(t))$,
a : related to proliferative ability of cells
⇒ the Gompertz model used to describe growth of tumors

$$N(t) = K \exp[\log(N(0)/K) \exp(- a \, t)]$$

N(0): size of tumor at the start of observation
K: maximum size that can be reached by tumor given available nutrients

A fundamental difference with logistic model is that growth rate is unbounded when $N \to 0$

Deriving the Logistic equation

Note that in $dN/dt = B - D$ (B: total birth rate, D: total death rate)
$= bN - dN$ (b: per capita birth rate, d: per capita death rate)
$= (b - d) N = rN$
The birth and death rates were assumed to be density independent

Not true if resources for growth and reproduction are limited

So that $dN/dt = [b(N) - d(N)] N \equiv r(N) N$

With increased crowding, $b(N)$ should decrease as less food and fewer resources available for reproduction
E.g., we can choose a linear relation $b(N) = b - a N$
where b: per capita growth rate for unlimited resources
a: strength of density dependence

Similarly, with increased crowding, $d(N)$ should increase
E.g., assuming a linear relation $d(N) = d + c N$
where d: per capita death rate for unlimited resources
c: strength of density dependence

Special case:
Exponential growth when $a = 0$ and $c = 0$

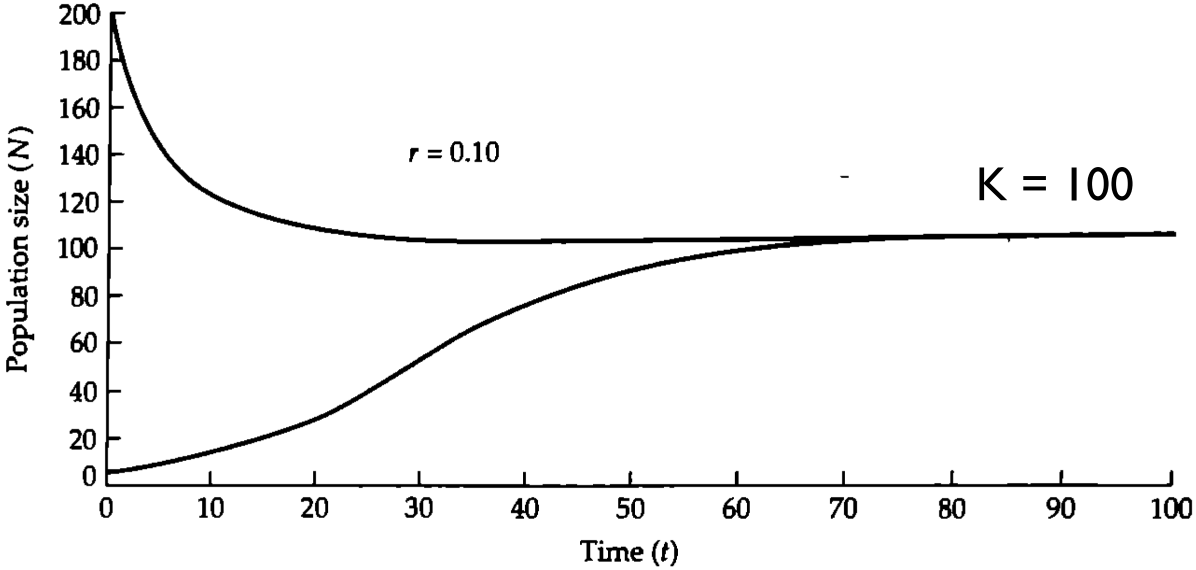
Deriving the Logistic equation

$$
\begin{aligned}
dN/dt &= [\,(b - a\,N) - (d + c\,N)\,]\,N \\
&= [(b - d) - (a + c)\,N]\,N \\
&= (b - d\,)\,N\,[1 - \{(a + c)/(b - d)\}\,N] \\
&= r\,N\,[1 - \{(a + c)/(b - d)\}\,N]
\end{aligned}
$$

Recall: $(b - d) \equiv r$

$\Rightarrow \quad dN/dt = r\,N\,[\,1 - (N/K)]$

where $K = (b - d)/(a + c)$ is the carrying capacity, the max population size that can be supported



K = 100

Image: Gotelli, *A Primer of Ecology* (2001)

Fixed points occur at N* = 0 and N* = K, as found by setting dN/dt = 0 and solving for N

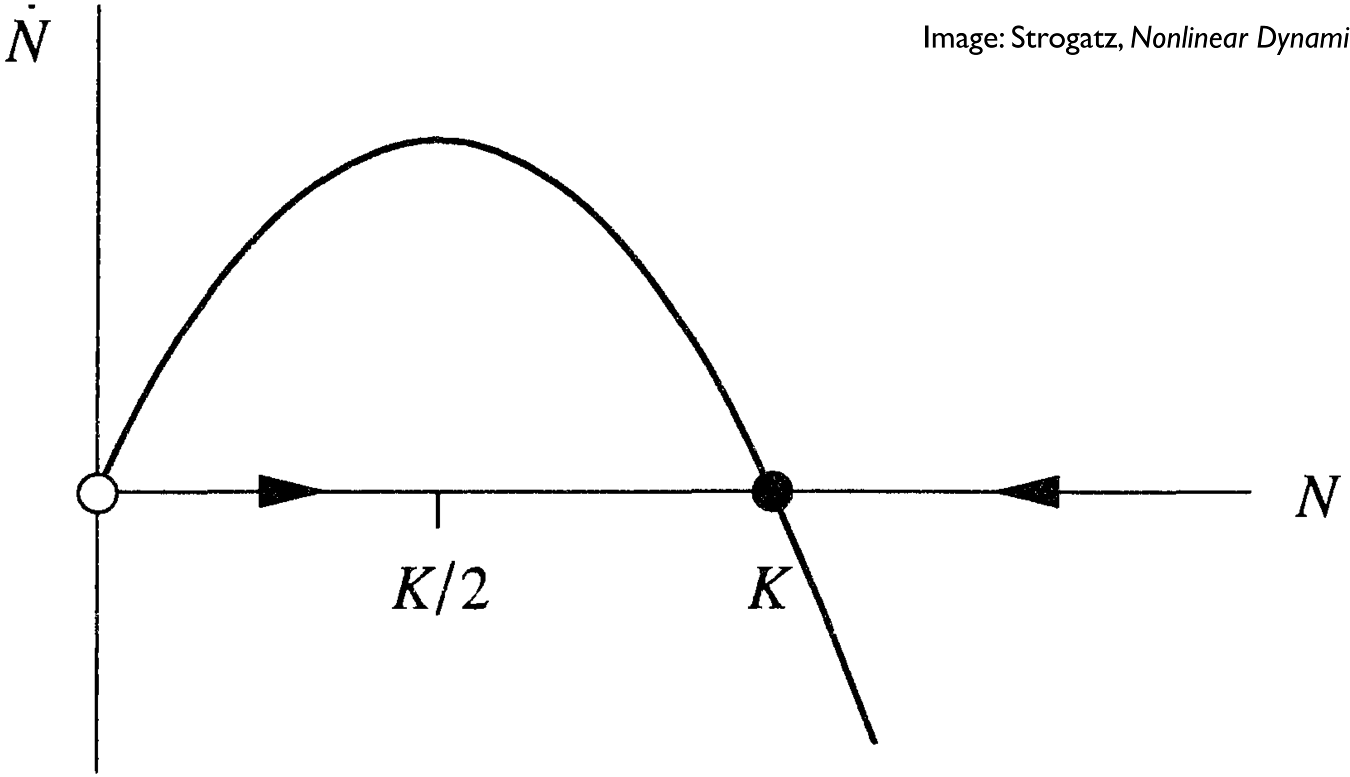


Image: Strogatz, *Nonlinear Dynamics and Chaos*

N* = 0 : unstable fixed point
N* = K : stable fixed point.

the population always approaches the carrying capacity if N>0

Closed form solution of the Logistic eqn

$N = N_0$ at $t=0$

$$dN/dt = r\,N\,[\,1 - (N/K)] = r\,N\,[K - N]/K$$

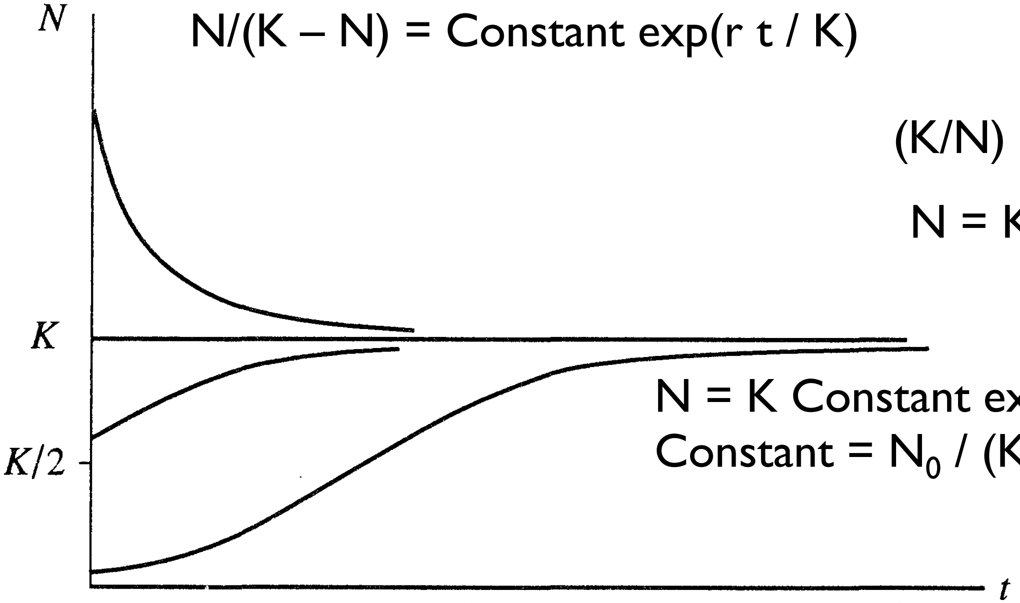
$$dN/\,(N\,[\,K - N]) = r\,dt\,/\,K$$

$$\int dN/\,(N\,[\,K - N]) = \int r\,dt\,/\,K$$

$$(1/K)\,[(\int dN/N) + (\int dN/\{K - N\})] = \int r\,dt\,/\,K$$

$$(1/K)\,[\ln(N) - \ln(K - N)] = (r\,t\,/\,K) + \text{constant}$$

$$\ln[N/(K - N)] = (r\,t\,/\,K) + \text{constant}$$



$$N/(K - N) = \text{Constant}\,\exp(r\,t\,/\,K)$$

$$(K/N) = 1 + [1/\text{Constant}\,\exp(r\,t\,/\,K)]$$

$$N = K/\{1 + [1/\text{Constant}\,\exp(r\,t\,/\,K)]\}$$

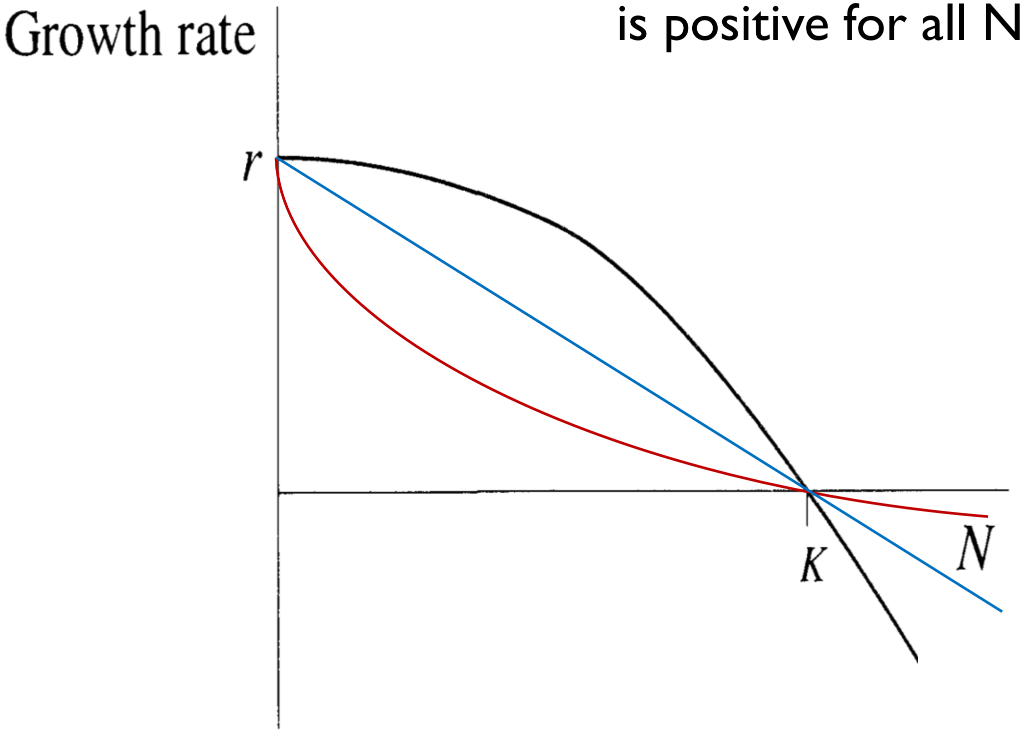
$$N = K\,\text{Constant}\,\exp(r\,t\,/\,K)\,/\,[1 + \text{Constant}\,\exp(r\,t\,/\,K)]$$

$$\text{Constant} = N_0\,/\,(K - N_0)$$

Image: Strogatz, *Nonlinear Dynamics and Chaos*

$$N\,(t) = K\,(N_0\,/\,(K - N_0))\exp(r\,t\,/\,K)\,/\,[1 + (N_0\,/\,(K - N_0))\,\exp(r\,t\,/\,K)]$$

Logistic-like models : per capita rate of change of population r (t) has a maximum at $N = 0$, is positive for all N < K, and negative for all N > K.

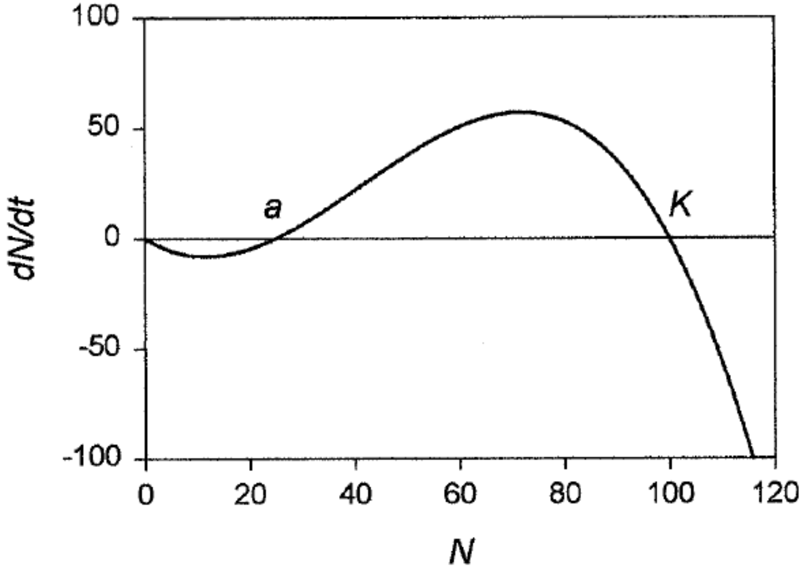


Non-logistic population growth

Example: Allee effect

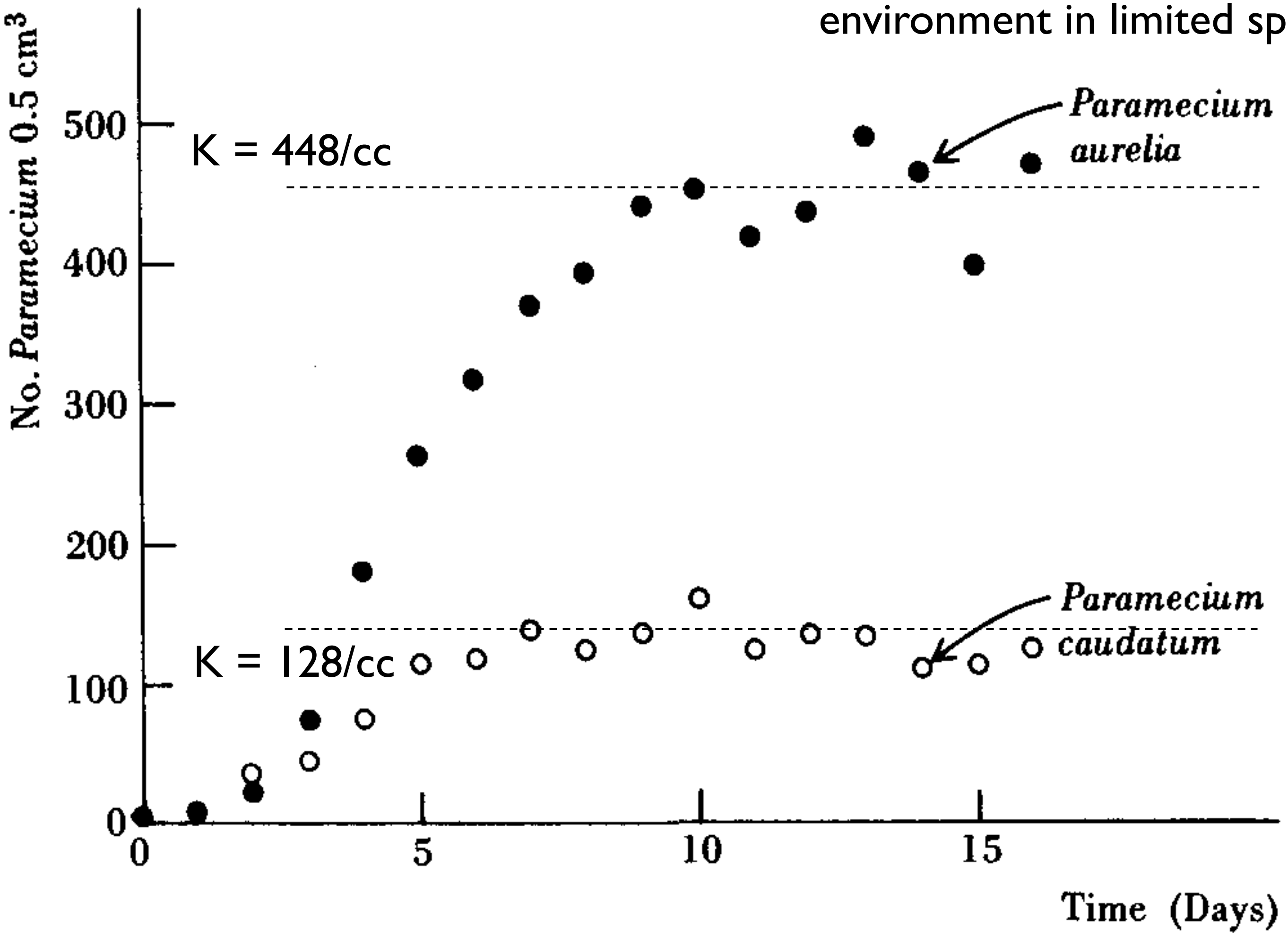
Per capita rate of change increases for small N, reaches a peak at some intermediate N, and declines thereafter.

Figure: Turchin, Complex Population Dynamics



Does population growth follow the logistic equation?

Gause’s experiments on the growth of protozoa populations under conditions of constant environment in limited space



K = 448/cc

K = 128/cc

Figure: Gause, *The Struggle for Existence* (1934)

Discretizing the logistic equation

First approach: $\frac{\Delta N}{\Delta t} \approx \frac{dN}{dt} = r_0 N\left(1 - \frac{N}{k}\right)$

set $\Delta t = 1$ (measured in generation units)

replace ΔN with $N_{t+1} - N_t$

$$N_{t+1} = aN_t - bN_t^2$$

$a = 1 + r_0$

$b = r_0/k$

Quadratic map

Second approach:

Integrate the logistic equation while assuming that the per capita growth rate r (t) is constant over the integration time-interval to obtain $N(t+1) = N(t)\exp[r(t)]$

substitute $r(t) = r_0(1 - N(t)/k)$ $\longrightarrow$ $N_{t+1} = N_t \exp\left[r_0\left(1 - \frac{N_t}{k}\right)\right]$ Ricker map

Time delay: Vital rates depend only on conditions at the beginning of the growth season

Third approach:

Integrate the logistic to obtain $N(t+1) = \frac{k}{1 + [(k - N(t)/N(t)]e^{-r_0}}$

substituting $\lambda_0 = \exp[r_0]$, $\longrightarrow$ $N_{t+1} = \frac{\lambda_0 N_t}{1 + [(\lambda_0 - 1)/k]N_t}$ Beverton-Holt map

General approach for discretizing continuous time population dynamics models

Most population dynamical models have the form :

$$\frac{dN}{Ndt} = f(\text{all sorts of stuff})$$

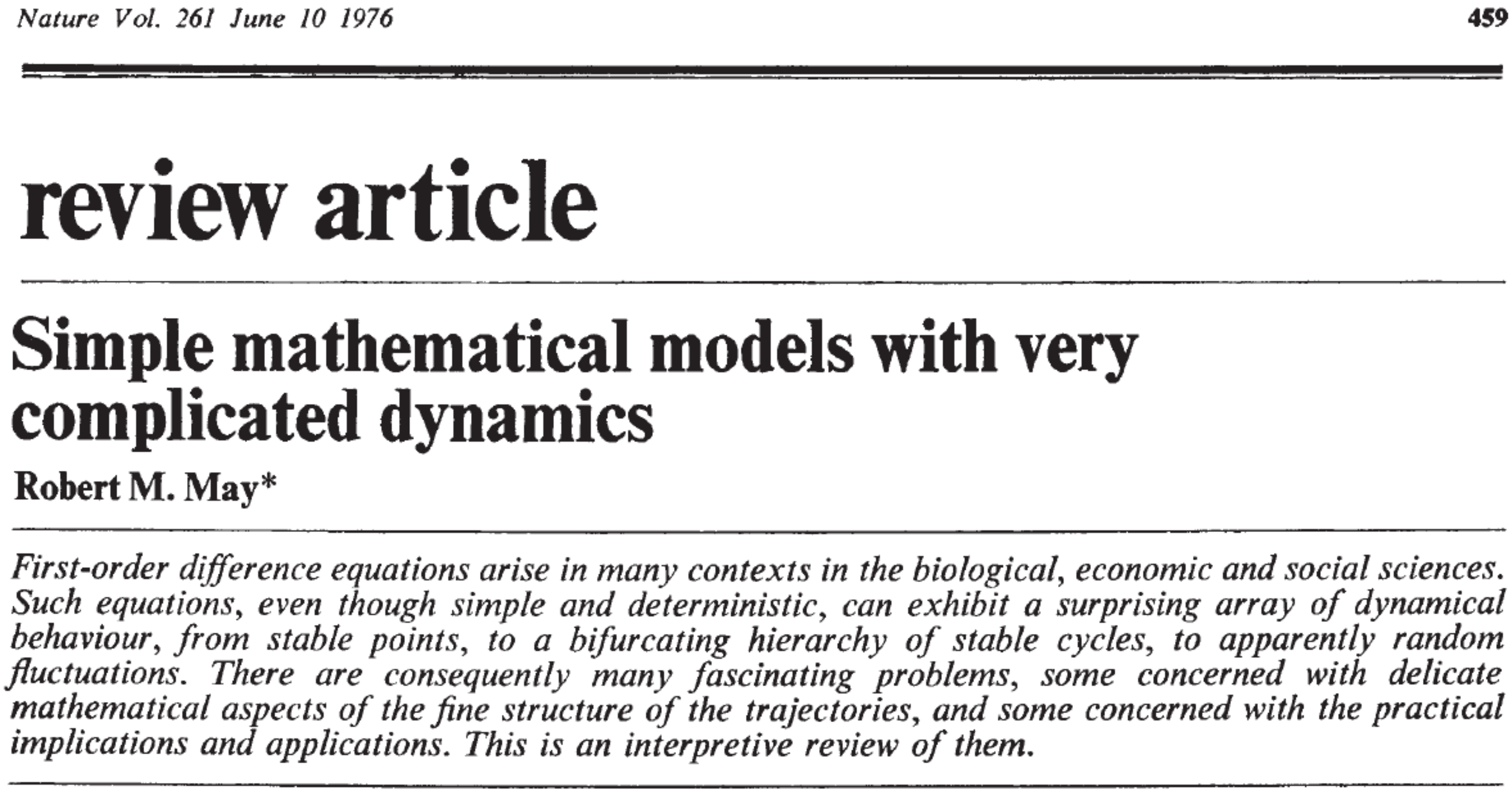
Approximate as:

$$N_{t+1} = N_t \exp[f(\text{all sorts of stuff})]$$

Third approach is the most accurate one, but explicit solutions for nonlinear dynamical models are often unavailable

Quadratic map

$$N_{t+1} = \lambda_0 N_t (1 - N_t / k)$$



Nature Vol. 261 June 10 1976 **459**

review article

Simple mathematical models with very complicated dynamics

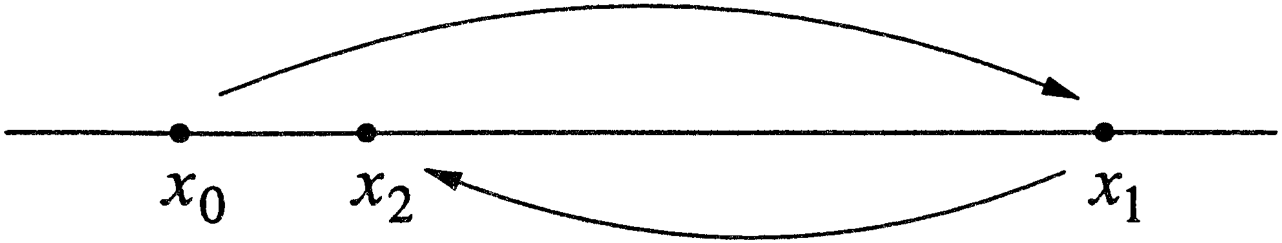
Robert M. May*

First-order difference equations arise in many contexts in the biological, economic and social sciences. Such equations, even though simple and deterministic, can exhibit a surprising array of dynamical behaviour, from stable points, to a bifurcating hierarchy of stable cycles, to apparently random fluctuations. There are consequently many fascinating problems, some concerned with delicate mathematical aspects of the fine structure of the trajectories, and some concerned with the practical implications and applications. This is an interpretive review of them.

A map can exhibit more complex behavior than an ODE

Figures: Strogatz, *Nonlinear Dynamics and Chaos*

vs

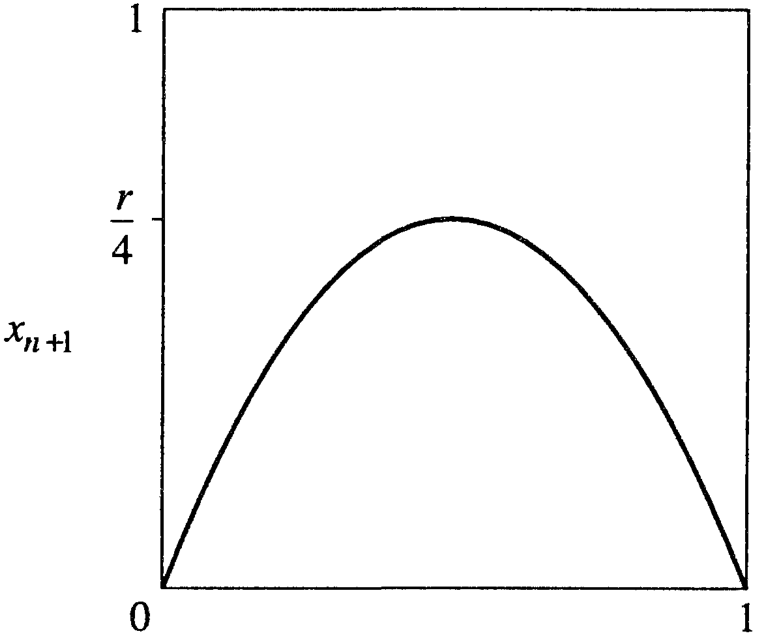


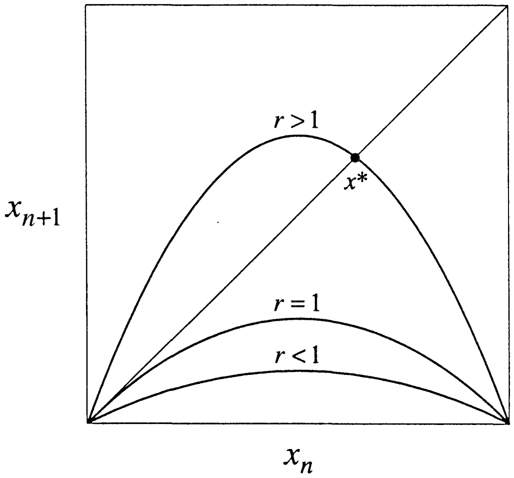
The system hops from one state to another rather than flowing continuously along the phase space

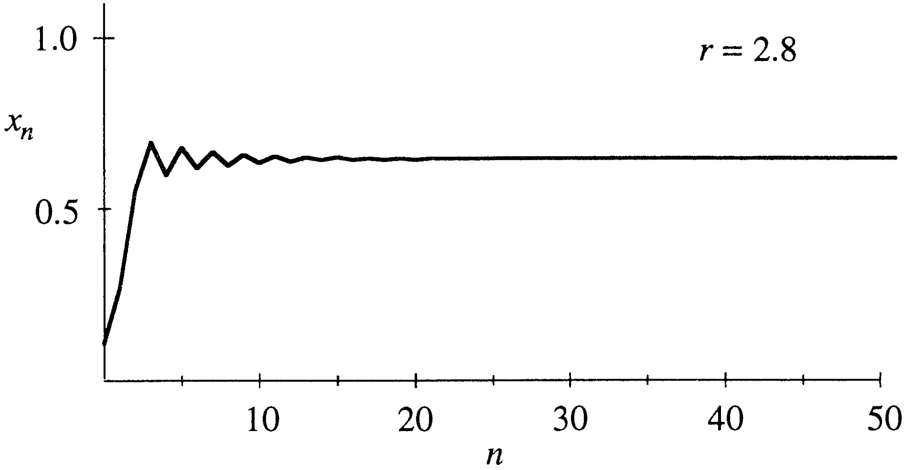
Quadratic map

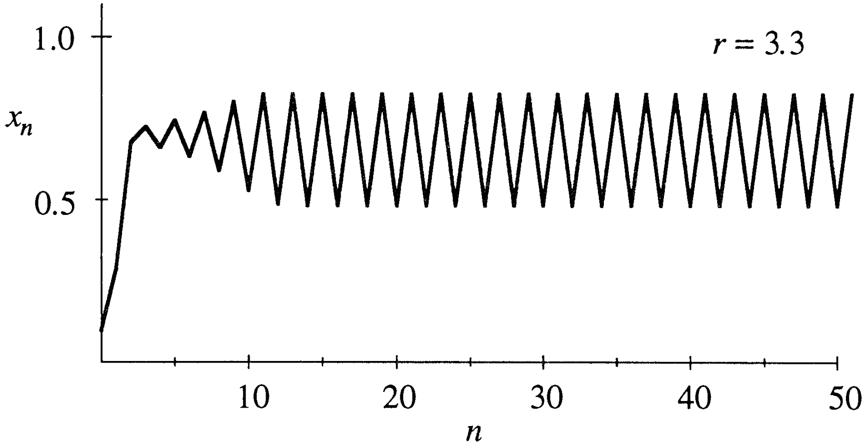
$$x_{n+1} = rx_n(1 - x_n)$$

Figures: Strogatz, *Nonlinear Dynamics and Chaos*

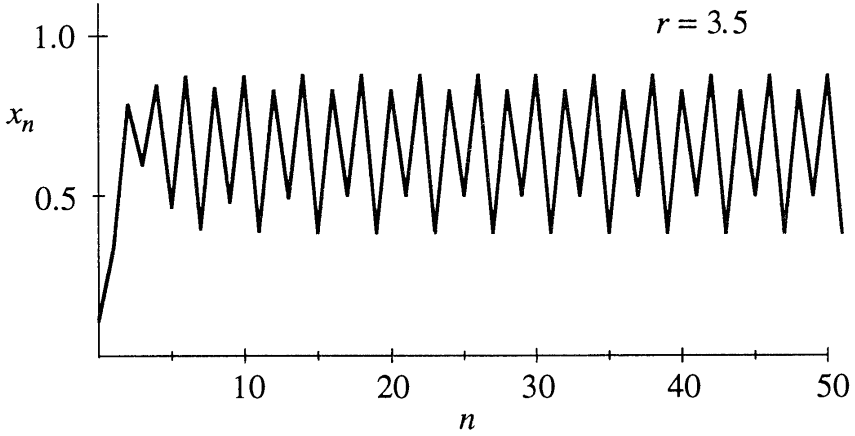








Period doubling in Quadratic map



$r_1 = 3$	(period 2 is born)
$r_2 = 3.449...$	4
$r_3 = 3.54409...$	8
$r_4 = 3.5644...$	16
$r_5 = 3.568759...$	32
$\vdots$	$\vdots$
$r_\infty = 3.569946...$	∞

Figures: Strogatz, *Nonlinear Dynamics and Chaos*

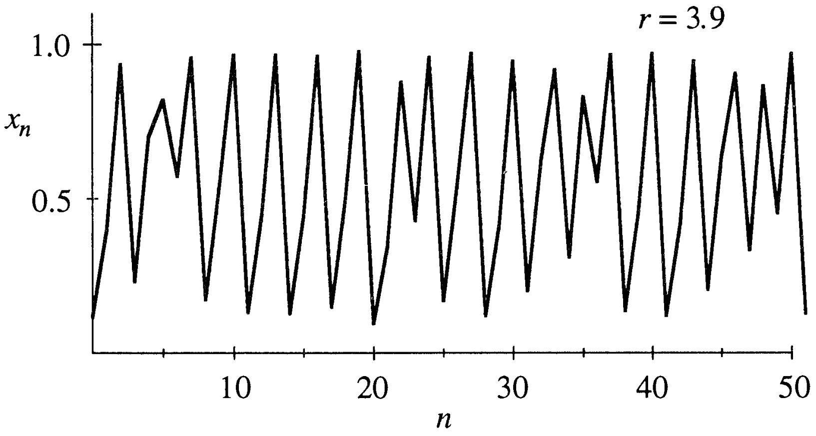
The interval between successive bifurcations decreases rapidly, converging to the limiting value of 3.569946.. Geometrically

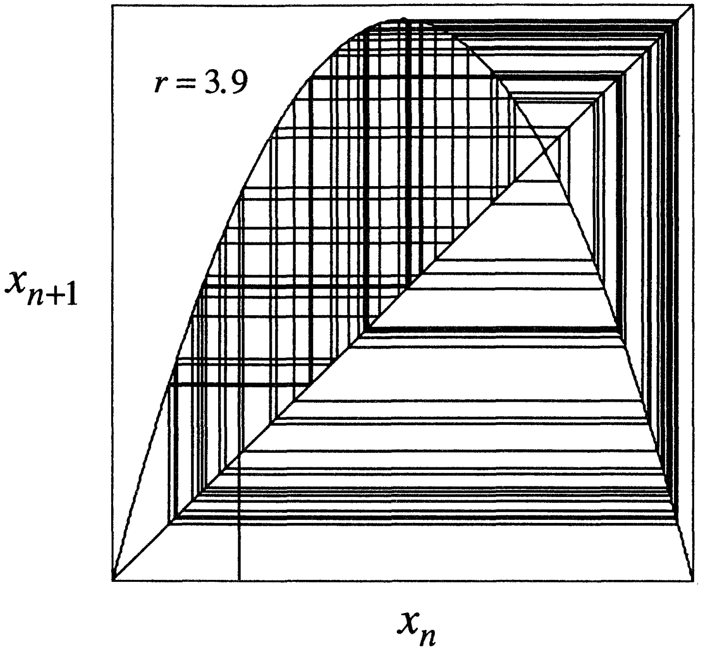
In the limit of large n, the gap between successive transitions decreases by the constant factor (Feigenbaum constant):

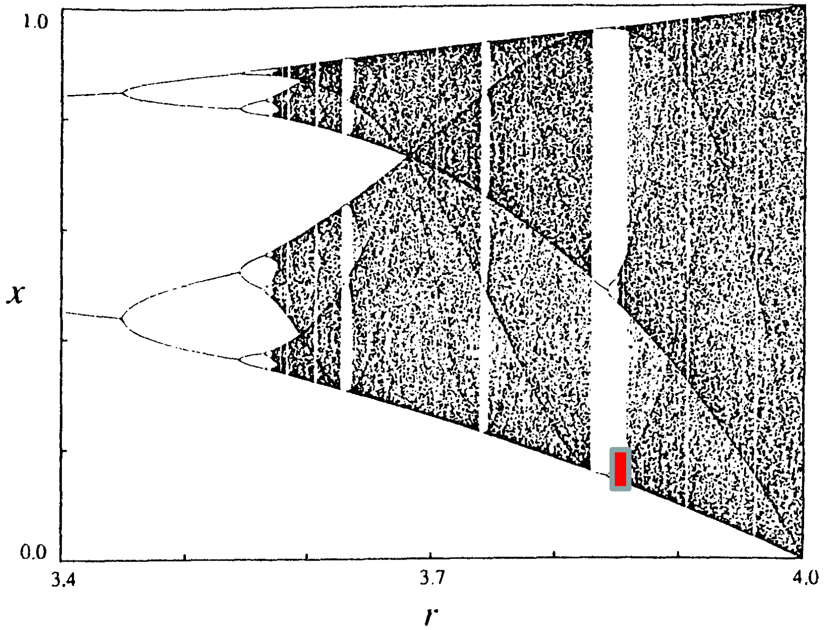
$$\delta = \lim_{n\to\infty} \frac{r_n - r_{n-1}}{r_{n+1} - r_n} = 4.669\ldots.$$

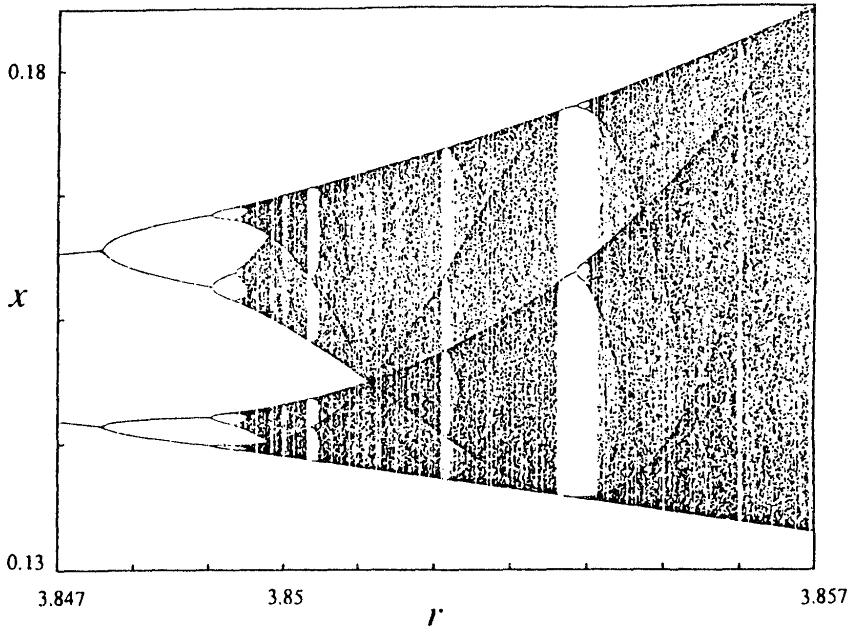
Mitchell Feigenbaum (1944-2019)

Chaos









Figures: Strogatz, *Nonlinear Dynamics and Chaos*

Figures: Strogatz, *Nonlinear Dynamics and Chaos*

Measuring Chaos: Liapunov exponent

$$\lambda = \lim_{n\to\infty} \left\{ \frac{1}{n} \sum_{i=0}^{n-1} \ln\left|f'(x_i)\right| \right\}$$

Exponential divergence of nearby trajectories

$$\left|\delta_n\right| \approx \left|\delta_0\right| e^{n\lambda}$$

$$\begin{aligned}
\lambda &\approx \frac{1}{n} \ln\left|\frac{\delta_n}{\delta_0}\right| \\
&= \frac{1}{n} \ln\left|\frac{f^n(x_0+\delta_0) - f^n(x_0)}{\delta_0}\right| \\
&= \frac{1}{n} \ln\left|(f^n)'(x_0)\right|
\end{aligned}$$

Expanding using the chain rule $(f^n)'(x_0) = \prod_{i=0}^{n-1} f'(x_i)$

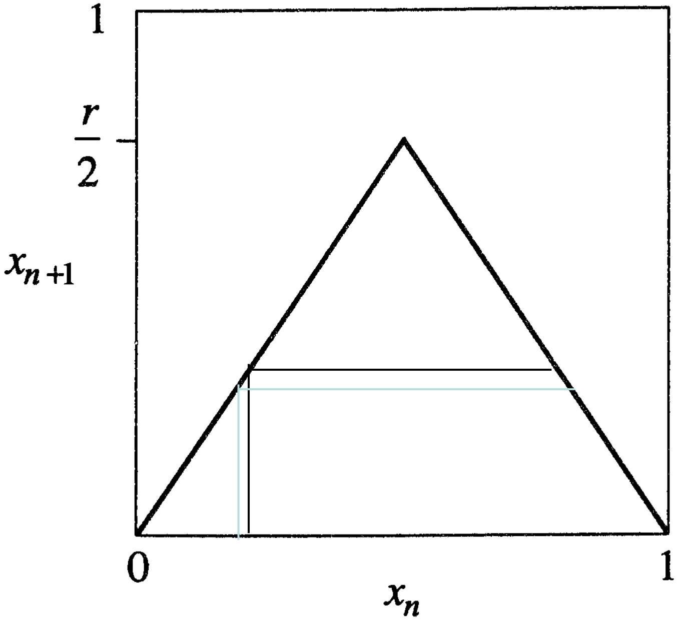
$$\begin{aligned}
\lambda &\approx \frac{1}{n} \ln\left|\prod_{i=0}^{n-1} f'(x_i)\right| \\
&= \frac{1}{n} \sum_{i=0}^{n-1} \ln\left|f'(x_i)\right|.
\end{aligned}$$

Figure: Strogatz, *Nonlinear Dynamics and Chaos*

Measuring Chaos: Tent map

$$f(x)=\begin{cases} rx, & 0\le x\le \frac{1}{2} \\ r-rx, & \frac{1}{2}\le x\le 1 \end{cases}$$

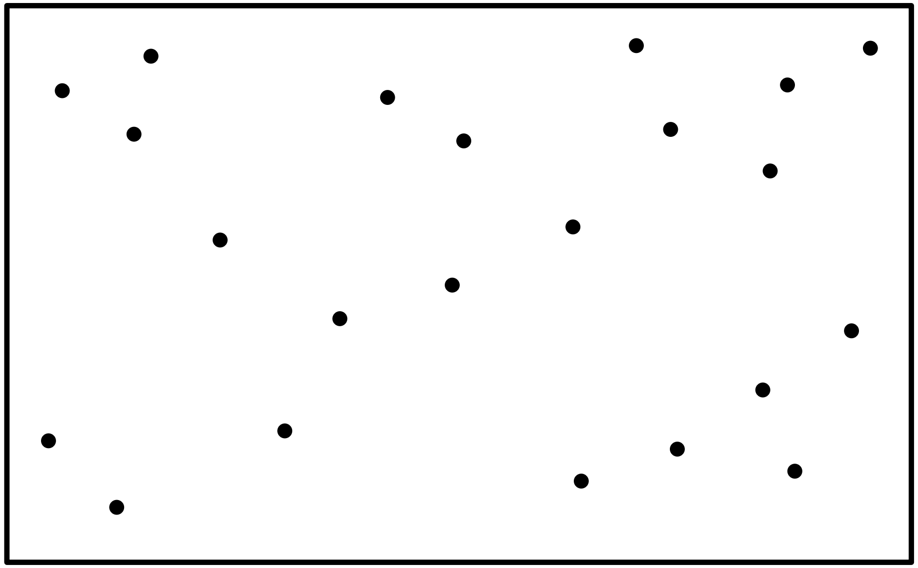
for $0\le r\le 2$ and $0\le x\le 1$



$$\lambda = \ln r > 0$$

Microscopic derivation of the logistic (Ricker) map

- Consider a random distribution of individual organisms (represented by points) over an available resource.
- Each individual has a minimum sufficient resource requirement to survive and reproduce normally.
- Survival and reproduction are adversely affected if the resource falls below a certain level, whereas a surplus has no influence.



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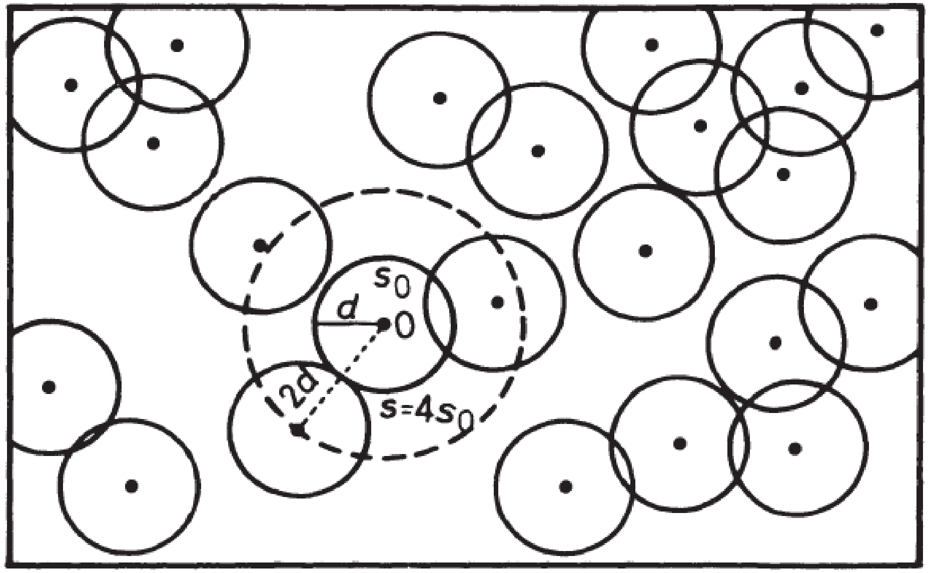


Royama, *Analytical Population Dynamics* (1992)

A circle of radius d around each point represents a minimum sufficient area s_0 for each individual to secure its minimum sufficient requirement n, given resource density, i.e., amount available per unit habitat space, D

$\Rightarrow D\, s_0 = n$

If circles overlap with each other, the corresponding points compete for the resource. The individuals that a given individual (point 0, say) competes with are those that fall within the concentric dashed circle with radius 2 d and area $s = 4\, s_0$.

Taking into account the spatial distribution

Let r_i : average reproductive rate of individuals having i competitors

$Pr(i)$: the expected proportion of individuals having i competitors

Then, the *mean reproductive rate* $r(t)$ $(= x_{t+1}/x_t)$ of the population is given by the weighted sum

$$r(t) = r_0\, Pr(0) + r_1\, Pr(1) + r_2\, Pr(2) + \ldots + r_i\, Pr(i) + \ldots$$

Ignoring the time indices in the $r_0, r_1, r_2, \ldots$

Consider the individuals to be scattered across space following a

Poisson distribution with mean density x.

Poisson distribution

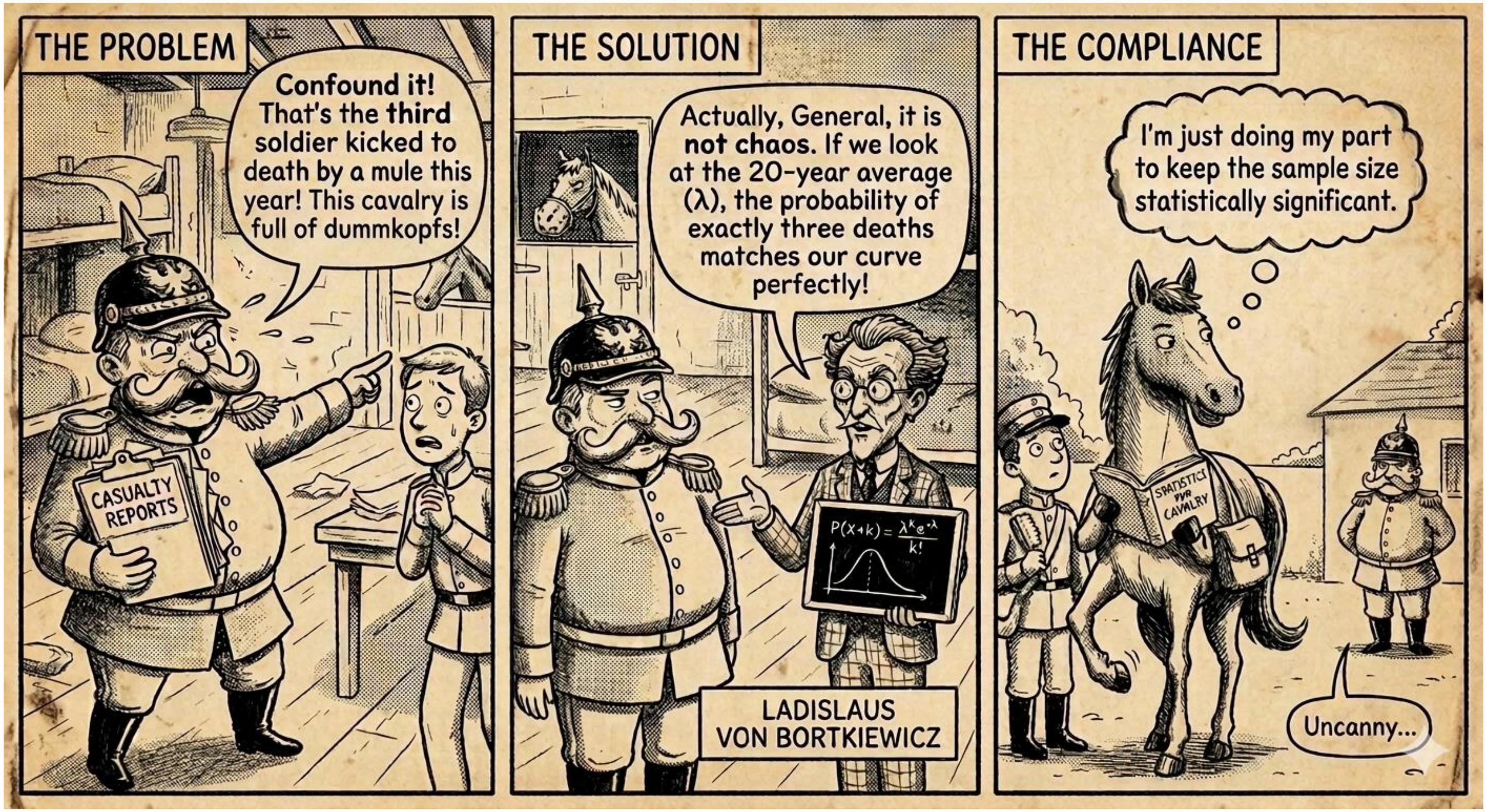


Image: Nano Banana 2 image generator

The probability of observing exactly k events

$$P\,(\,x = k\,) = \frac{\lambda^k\, e^{-\lambda}}{k!}$$

λ : mean rate of event

Conditions

- Events are rare: The probability of each event happening is extremely small
- Events are independent: One event doesn't make the next event any more or less likely.
- The average rate (λ) is constant

Taking into account the spatial distribution

Let r_i : average reproductive rate of individuals having i competitors
Pr(i) : the expected proportion of individuals having i competitors

Then, the *mean reproductive rate* r(t) (= x_{t+1}/x_t) of the population is given by the weighted sum

$$r(t) = r_0\, Pr(0) + r_1\, Pr(1) + r_2\, Pr(2) + \dots + r_i\, Pr(i) + \dots$$

Ignoring the time indices in the $r_0, r_1, r_2, \dots$

Consider the individuals to be scattered across space following a **Poisson distribution** with mean density *x*.

⇒ the number of points within each circle of area *s* (excluding the point at the centre) is also Poisson distributed with the mean $\lambda = s\, x$

⇒ the expected proportions are

$$Pr\,(\,i\,) = \frac{sx^i\, e^{-sx}}{i!}\,, \quad i = 0, 1, 2, \dots$$

Substituting

$$r_t = r_0 \exp(-s\, x_t) + r_1\, (s\, x_t) \exp(-s\, x_t) + r_2\, (s\, x_t)^2 \exp(-s\, x_t)/2! +$$

$$r_t = r_0 \exp(-s\, x_t)\, [\, 1 + (r_1 / r_0)(s\, x_t) + (r_2 / r_0)\, (s\, x_t)^2 / 2! + \dots]$$

Decreasing reproduction rate with increasing competition

As the number of competitors i increases for an individual, its reproductive rate r_i decreases because of decreased resource.

Assume that the addition of an extra competitor to the existing i competitors within the circle of area s reduces the reproduction rate of the individual by a factor k (≤ 1)

$\Rightarrow r_i = r_{i-1}\,k = r_{i-2}\,k^2 = \ldots = r_0\,k^i$

We identify $r_0 \equiv r_m$, the biologically realizable maximum reproductive rate

Substituting in

$$r_t = r_0 \exp(-s\,x)\,[\,1 + (r_1 / r_0)(s\,x) + (r_2 / r_0)\,(s\,x)^2 / 2! + \ldots\,]$$

We get

$$r_t = r_m \exp(-s\,x_t)\,[\,1 + k\,s\,x_t + (k\,s\,x_t)^2 / 2! + \ldots\,]$$

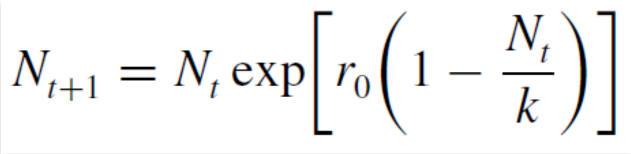
But $\exp(k\,s\,x_t) = 1 + k\,s\,x_t + (k\,s\,x_t)^2 / 2! + \ldots$

$$= r_m \exp(-s\,x_t)\exp(k\,s\,x_t)$$

$$= r_m \exp(-c\,x_t) \qquad \text{where } c \equiv (1-k)\,s$$

$$\Rightarrow \boxed{x_{t+1} / x_t = \exp(R_m\,[\,1 - (c\,x_t / R_m)]\quad \text{where } R_m \equiv \log(r_m)}$$

Compare with



$$N_{t+1} = N_t \exp\left[r_0\left(1 - \frac{N_t}{k}\right)\right]$$

Ricker map