Single-Species Population Models

- Birth & Death in a population

Let $N(t)$ = Size of a population

b = per capita birth rate (expected number of offspring per individual per unit time)

d = per capita death rate (probability of mortality per individual per unit time)

If $b(N)$ ($d(N)$) then the birth (death) rate is density-dependent

Birth (death) rates for the population are given by bN (dN)

The intrinsic growth rate is given by

$$r = \max_N \{ b(N) - d(N) \}$$

$= b - d$ if birth/death rate is density-independent

Density-Dependent Fecundity
= Birth

(2)

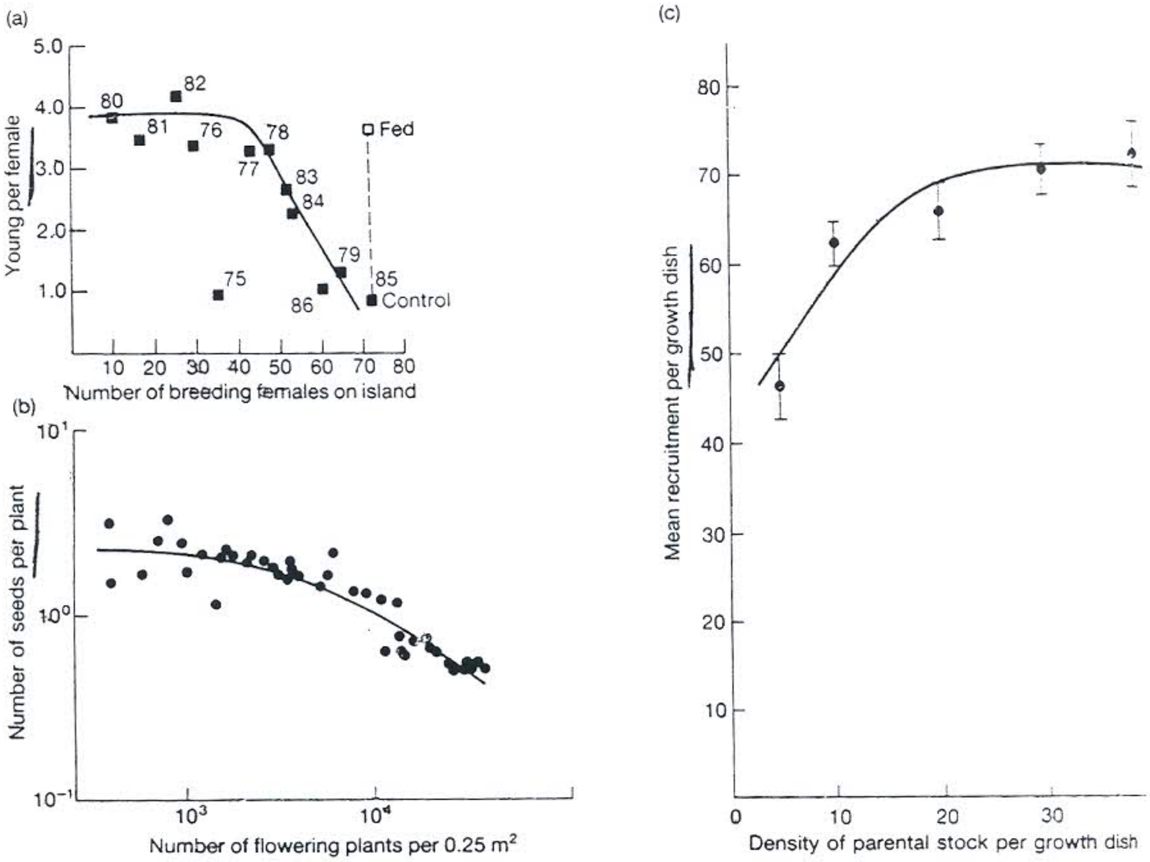


Figure 6.4. Density-dependent fecundity. (a) In the population of song sparrows, *Melospiza melodia*, on Mandarte Island, BC, Canada, fecundity changes from density-independence to overcompensating density-dependence as density increases, over the years 1975–1986. (For instance, at a density of 40, the total number of young produced was roughly $40 \times 4 = 160$, whereas at a density of 70 it was roughly $70 \times 1 = 70$.) Providing supplementary food in 1985 suggested that competition for food was the cause (Arcese & Smith, 1988). (b) In the annual dune plant *Vulpia fasciculata*, fecundity changes from approximate density-independence to undercompensating density-dependence. (After Watkinson & Harper, 1978. From Watkinson & Davy, 1985.) (c) In the fingernail clam, *Musculium securis*, fecundity changes from undercompensating density-dependence to nearly exactly compensating density-dependence (Mackie *et al.*, 1978).

Density-Dependent Mortality
= Death

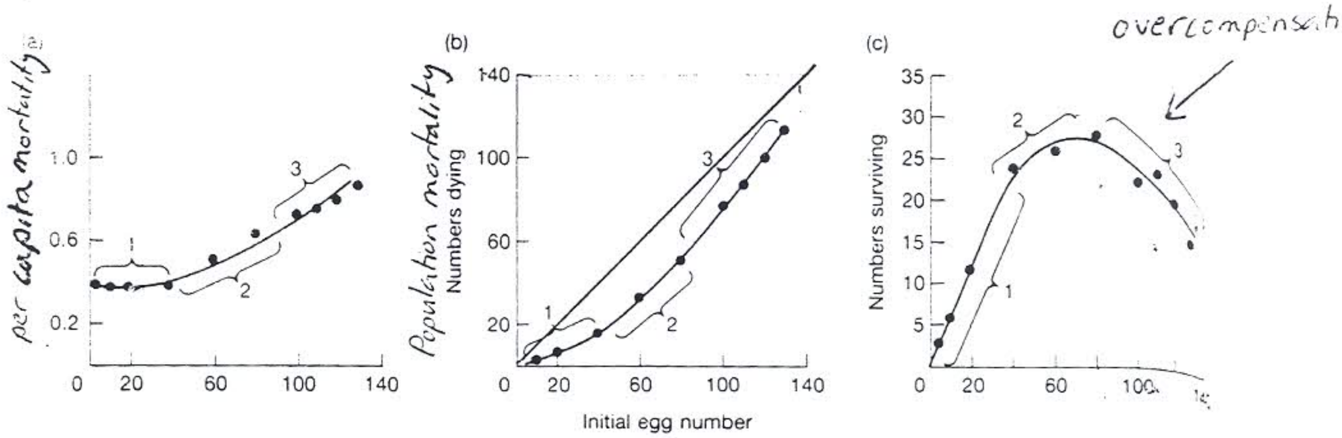


Figure 6.1. Density-dependent mortality in the flour beetle *Tribolium confusum* (a) as it affects mortality rate, (b) as it affects the numbers dying, and (c) as it affects the numbers surviving. In region 1 mortality is density-independent; in region 2 there is undercompensating density-dependent mortality; in region 3 there is overcompensating density-dependent mortality. (After Bellows, 1981.)

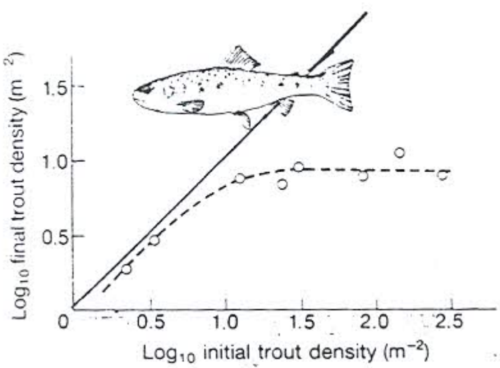


Figure 6.2. Density-dependent mortality amongst trout fry. At high trout densities the increasing mortality rate compensates exactly for increasing trout density and a constant number of trout survive. (After Le Cren, 1973. From Hassell, 1976.)

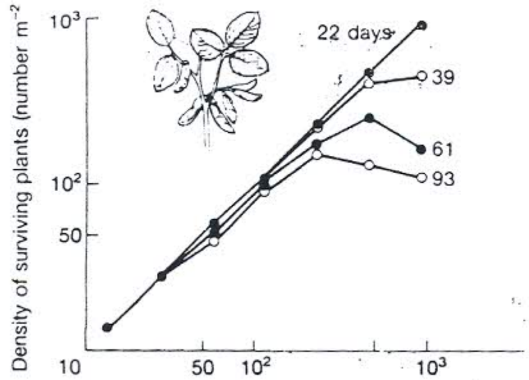
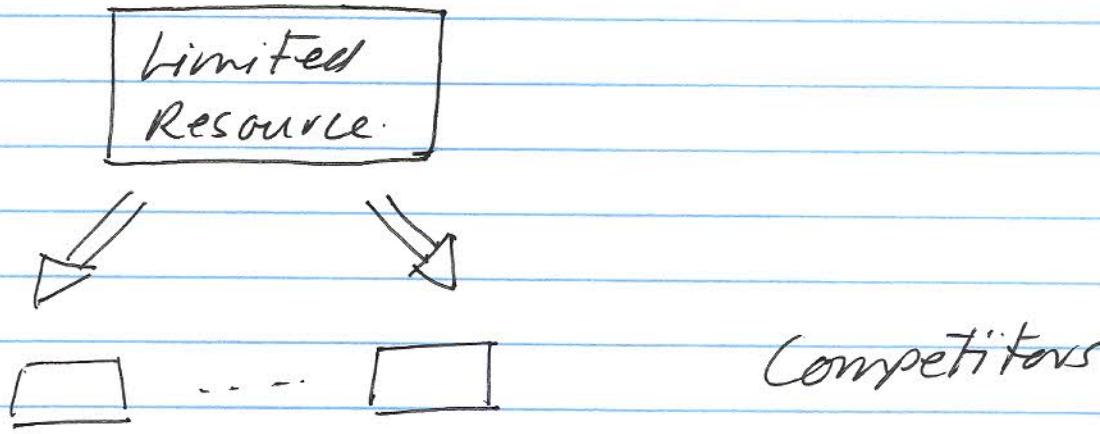


Figure 6.3. Density-dependent mortality in the soybean (*Glycine soja*). After 61 and 93 days the increasing mortality rate overcompensates for increases in sowing density, and the number of surviving plants declines. (After

What are the causes for density-dependent birth & death?

A) Intraspecific competition

I Exploitation Competition

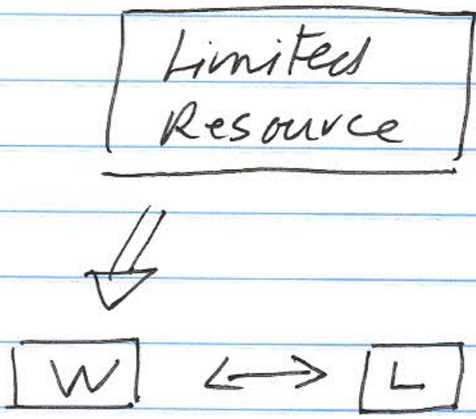


The more resource one individual gets, the less others do

Eg Flour beetle (Tribolium confusum)

Beetles compete for flour. If there is insufficient flour per beetle then all can die before reaching the adult stage

II Interference competition



Direct contest between competitors & the winner takes the resource.

Eg Competition for a limited number of territories. Winners have access to food & reproductive resources.

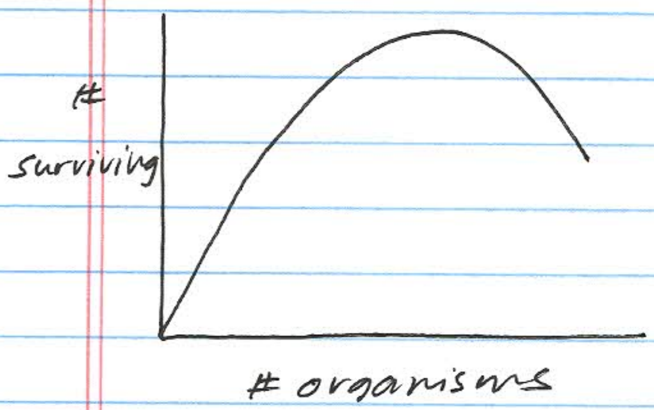
Note: The kind of competition may determine the form of density-dependence

- Exploitation competition may give rise to overcompensation in discrete-time models

vs.

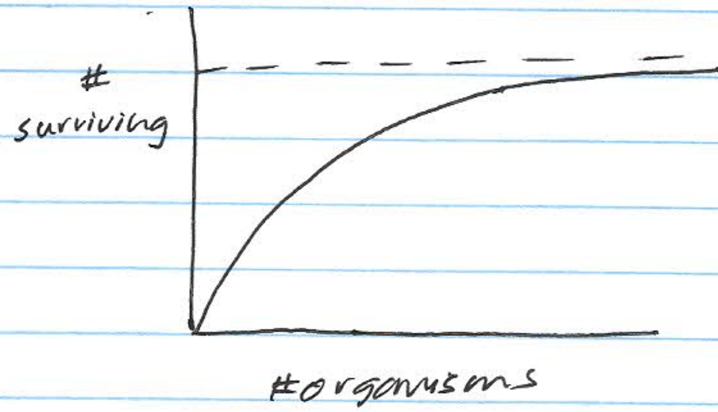
- Interference competition gives rise to compensation.

Overcompensation



(Exploitation)

Compensation

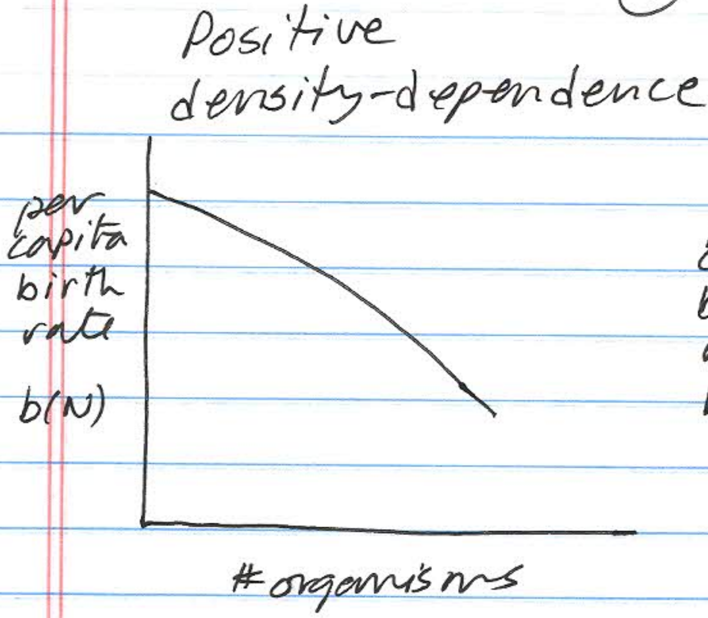


(Interference)

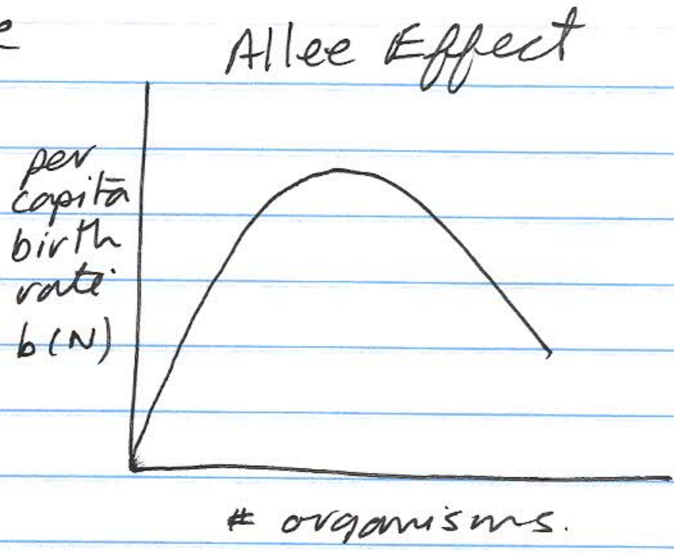
B) <u>Intra</u>specific cooperation

<u>Eg</u> - sexual reproduction
- increased feeding efficiencies in groups (aphids, wolves)
- antipredator defenses (vigilance in birds, schooling in fish etc.)

cooperation may determine the form of the density-dependent birth / death rates.



(asexual reproduction)



(sexual reproduction – cooperation)

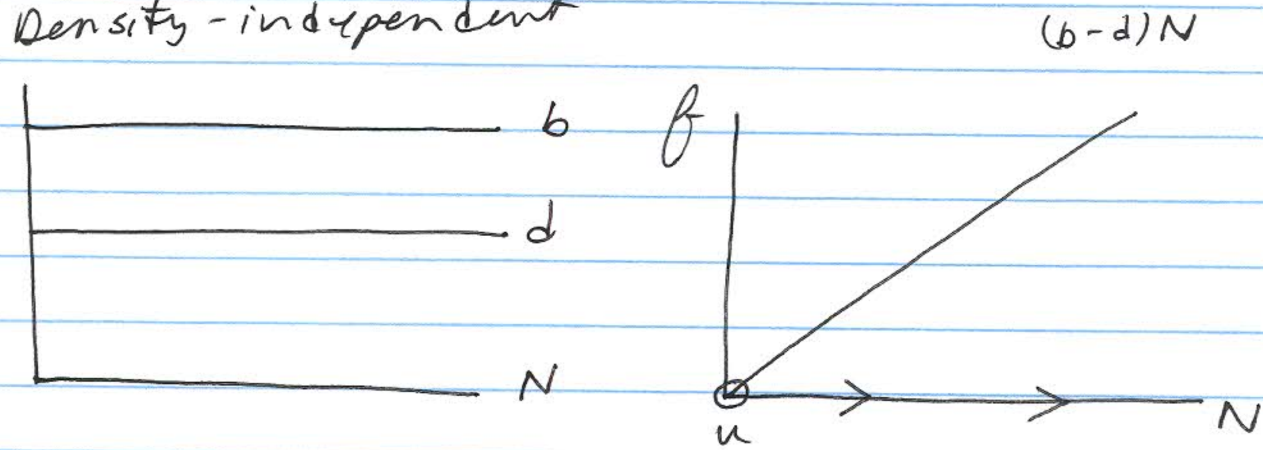
<u>Allee Effect:</u> Reduced per capita growth rate $(b(N) - d(N))$ at low densities / numbers.

Unstructured Population Models

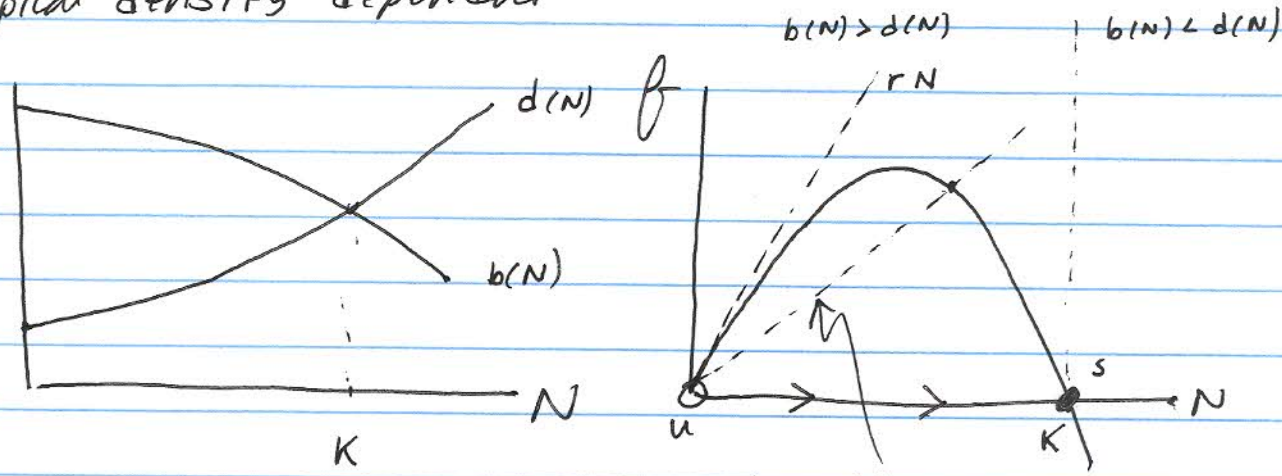
- Continuous-time deterministic model

$$\frac{dN}{dt} = N \underbrace{\left(b(N) - d(N) \right)}_{\text{per capita growth rate}} = f(N)$$

Density-independent



Typical density-dependent



slope is

$f(N)/N = b(N) - d(N)$

Here the intrinsic growth rate is

$$r = \max_N \{ f(N)/N \} = b(0) - d(0)$$

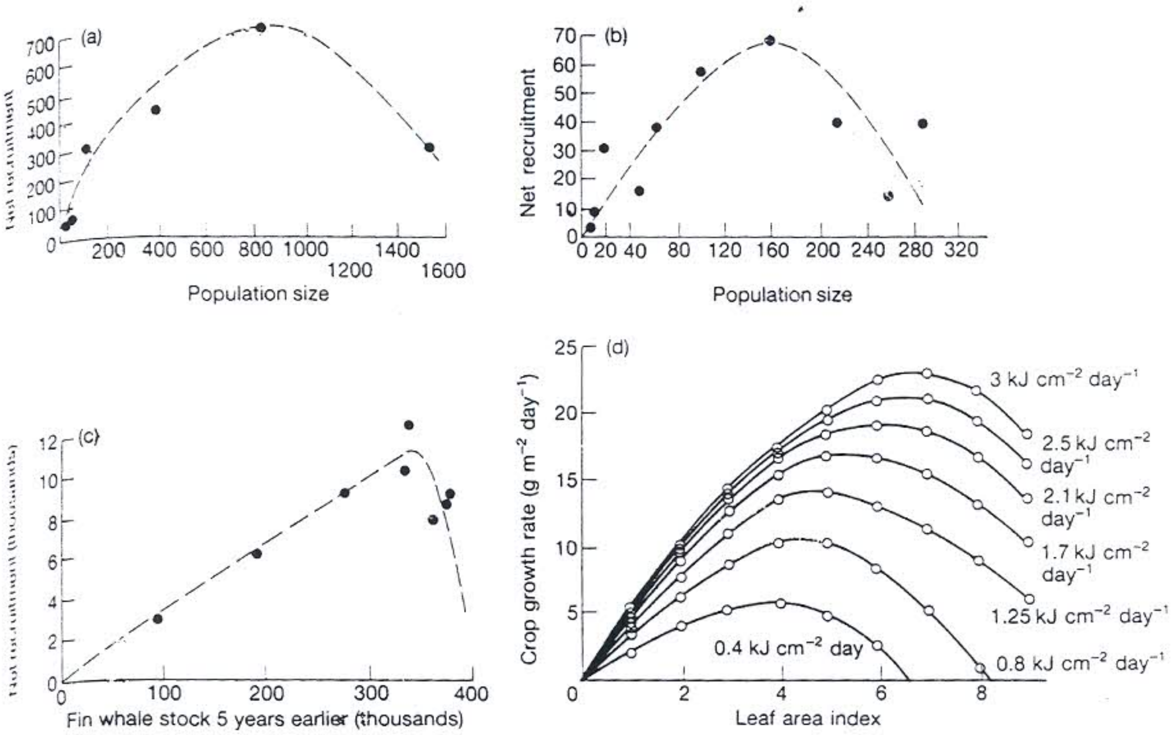
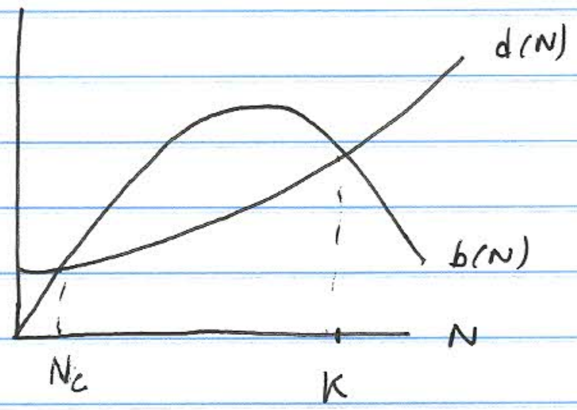
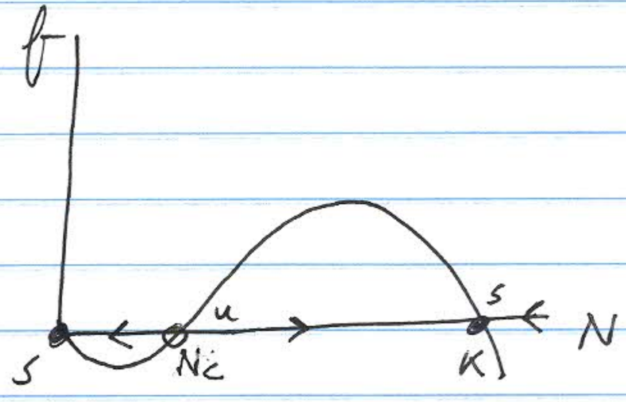


Figure 6.8. Some 'n'-shaped net recruitment curves, drawn by eye through the data points shown. (a) The ring-necked pheasant on Protection Island following its introduction in 1937. (Data from Einarsen, 1945.) (b) An experimental population of the fruit-fly *Drosophila melanogaster*. (Data from Pearl, 1927.) (c) Estimates for the stock of Antarctic fin whales. (After Allen, 1972.) (d) The relationship between crop growth rate of subterranean clover (*Trifolium subterraneum*) and leaf area index (LAI) at various intensities of radiation. Note that the leaf area index at which crop growth rate is maximal depends on the light intensity. (After Black, 1963.)

Cooperation



Allee dynamics



Malthus' Model

$$\frac{dN}{dt} = rN \qquad N(0) = N_0 \quad \text{initial pop'n size}$$

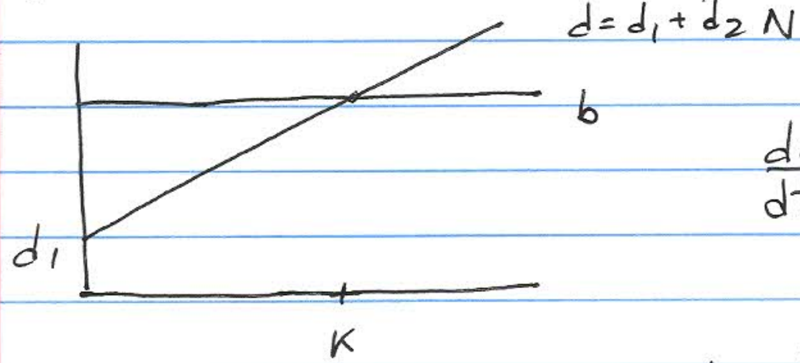
$$N(t) = N_0 e^{rt}$$

growth if $r > 0$ $(b > d)$
decline " $r < 0$ $(b < d)$

Malthus (1798) used this equation to model global human population growth

Density-dependent growth

Eg Logistic growth (Pearl Verhulst eq'n)



$$\frac{dN}{dt} = \left(b - (d_1 + d_2 N)\right) N$$

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

$$r = b - d_1 \qquad K = \frac{b - d_1}{d_2}$$

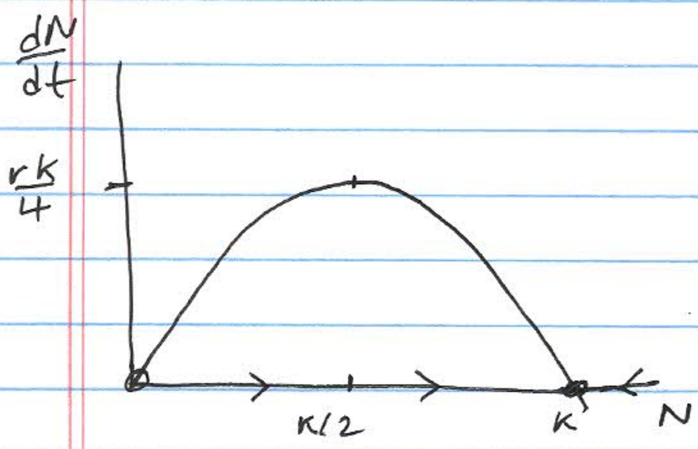
Sol'n $\dfrac{dN}{N(1-\frac{N}{K})} = r\,dt$ $\quad$ $\int$ using partial fractions . . .

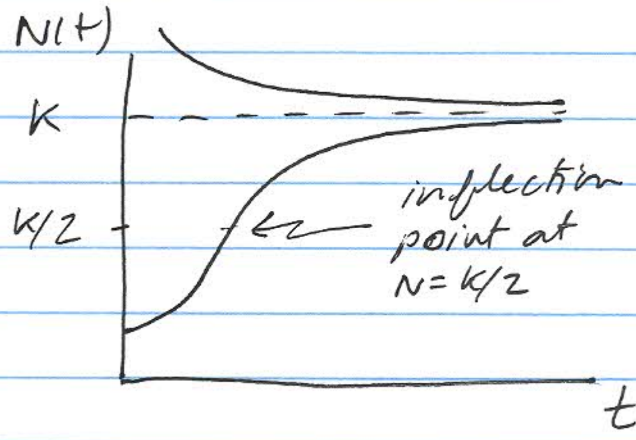
$N(0) = N_0$

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

1845 • Verhulst gave first modern treatment of this equation, but died in obscurity

1920s • Pearl & Reed discovered and advertized Verhulst's work.





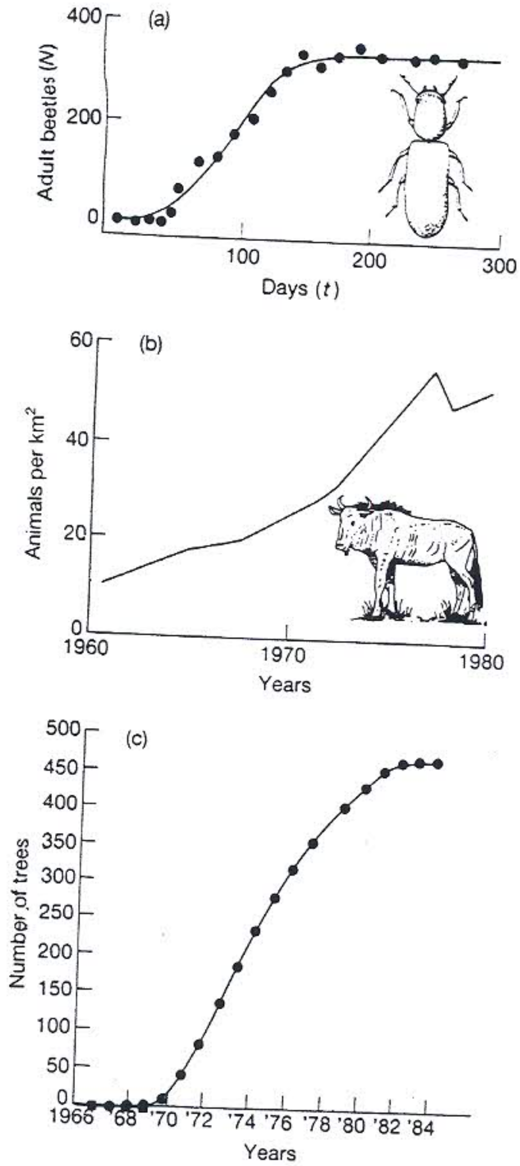
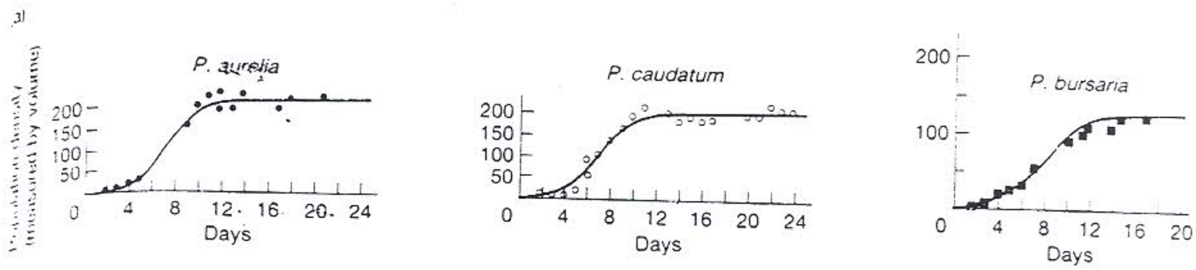


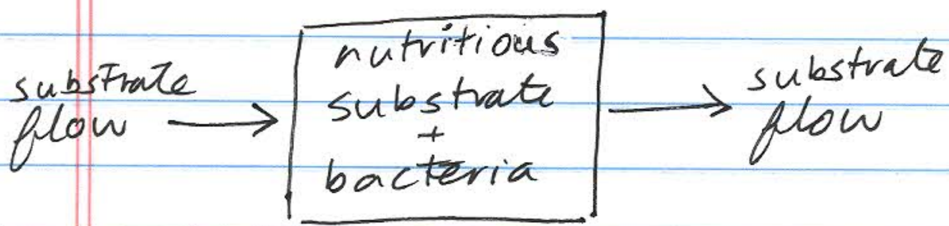
Figure 6.9. Real examples of an 'S'-shaped population increase. (a) The beetle *Rhizopertha dominica* in 10g of wheat grains replenished each week. (After Crombie, 1945.) (b) The population of wildebeest, *Connochaetes taurinus*, of the Serengeti region of Tanzania and Kenya seems to be levelling off after rising from a low density caused by the disease rinderpest. (After Sinclair & Norton-Griffiths, 1982. From Deshmukh, 1986.) (c) The population of the willow tree, *Salix cinerea*, in an area of land after myxamatosis had effectively prevented rabbit grazing. (After Alliende & Harper, 1989.)



Bacteria in a chemostat - <u>Model</u>

Exploitation competition in an explicit continuous-time model gives an explicit method for measuring r & K in logistic growth

Chemostat



$S(t)$ - conc. of substrate in chemostat
$N(t)$ - biomass of bacteria in chemostat
S_i - inflowing substrate conc.
D - dilution rate (= runoff rate)
Y - yield coefficient

Model

$$\dot{S} = D(S_i - S) - \frac{m}{Y} S N \qquad S(0) = S_0$$

$$\dot{N} = m S N - D N \qquad N(0) = N_0$$

Bacterial growth is modelled via <u>mass action</u>. It grows at rate mS & consumes Y^{-1} units of substrate to produce a unit of bacteria.

$$\dot{y} = m S_i (1-y) y - D y$$

$$= \underbrace{(m S_i - D)}_{r} y - \underbrace{m S_i}_{r/K} y^2$$

$$r = m S_i - D \qquad K = \frac{m S_i - D}{m S_i}$$

So we have come back to the logistic equation but with explicitly measured parameters.

Steady States (Critical Points) and Stability

<u>Defn</u> $N = N^*$ is an <u>equilibrium point</u> (steady state, critical point) for $\dot{N} = f(N)$ if $f(N^*) = 0$

<u>Defn</u> An equilibrium $N = N^*$ is <u>Liapunov stable</u> if a solution starting near N^* stays near N^* for all time.

IE if for all $\varepsilon > 0$ $\exists$ a $\delta > 0$ such that

$|N(0) - N^*| < \delta \Rightarrow |N(0) - N^*| < \varepsilon$ for all $t > 0$.

If, in addition $\lim_{t \to \infty} |N(t) - N^*| = 0$ then N^* is <u>locally</u> <u>asymptotically</u> <u>stable</u> (LAS).

<u>Defn</u> An equilibrium point N^* of $\dot{N} = f(N)$ is hyperbolic if $f'(N^*) \neq 0$

Theorem: Suppose N^* is a hyperbolic equilibrium of $\dot{N} = f(N)$ and that f has a continuous derivative, then N^* is LAS (unstable) if $\lambda = f'(N^*) < 0 \quad (>0)$.

Proof (Outline):

Linearize about $N = N^*$: $n = N - N^*$

$$\dot{n} = \dot{N} = f(N^* + n) = f(N^*) + f'(N^*)n + \mathcal{O}(n^2)$$
$$\approx f'(N^*)\, n$$

Thus n decays (grows) if $\lambda < 0$ ($\lambda > 0$).

Eg 1 Logistic Model

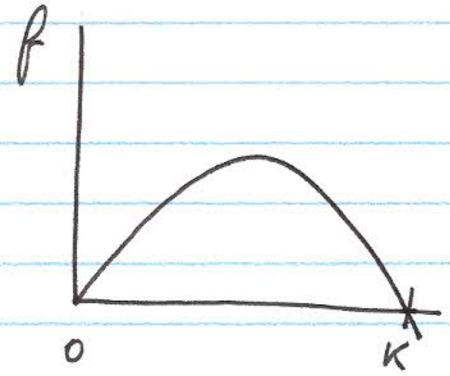
$$\dot{N} = rN\left(1 - \frac{N}{K}\right)$$

$N^* = 0 \quad \lambda_1 = f'(0) = r > 0$ origin is unstable

$N^* = K \quad \lambda_2 = f'(K) = -r < 0$ carrying capacity is LAS

Convex Growth Model

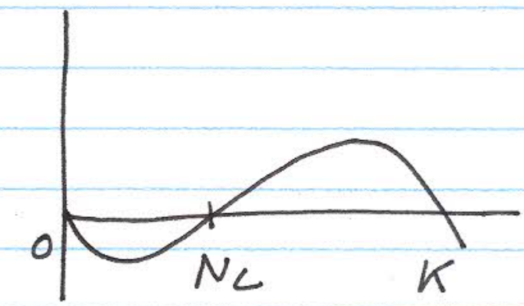
Eg 2



$f'(0) > 0$ unstable

$f'(K) < 0$ LAS

Allee dynamics



$f'(0) < 0$ LAS

$f'(N_c) > 0$ unstable

$f'(K) < 0$ LAS

Historical Aside: Population Growth

The following are five moments associated with population growth models

- Graunt (1662)
  - First modern day human demographer
  - Collected Bills of Mortality for London
  - Computed a doubling time of 64 years
  - Given Adam & Eve alive in 3948 BC

$$N = 2^{87.7} \approx 10^{26} \text{ people}$$

$$\approx 100 \text{ people/cm}^2$$

- Petty (1683)
  - Graunt forgot about the flood (2700 BC)
  - He also forgot about immigration from the countryside when calculating doubling times
  - Petty established a doubling time of

$T_D = 360 - 1200$ years $\quad N_0 = 8$

If $T_D = 360 \quad N = 8 \times 2^{12.2} \approx 37{,}000$

A variable doubling time gave

$N = 320 \times 10^6$ (just right)

Malthus (1798)

- Population grows geometrically
- Food grows arithmetically
  ⇒ Misery is inevitable
- Influenced Wallace & Darwin.

Verhulst (1845)

- First modern treatment of the logistic equation

Pearl & Reed (1920)

- Discovered & advertized Verhulst's work.
- Crusaded to declare logistic growth a "law of nature"
- Tried to fit all kinds of data to the logistic equation.