

**"Fifth Course on Mathematical Ecology
including and introduction to Ecological Economics"**

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**AGGREGATED COMMUNITY
MODELS**

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Two Species Community Models

- Let $\begin{cases} x_1 = x_1(t) \\ x_2 = x_2(t) \end{cases}$ be measurements of populations (numbers, density, biomass)
- Let $\begin{cases} B_i = B_i(x_1, x_2) \\ D_i = D_i(x_1, x_2) \end{cases}$ represent birth and death processes
- Per capita growth rates are

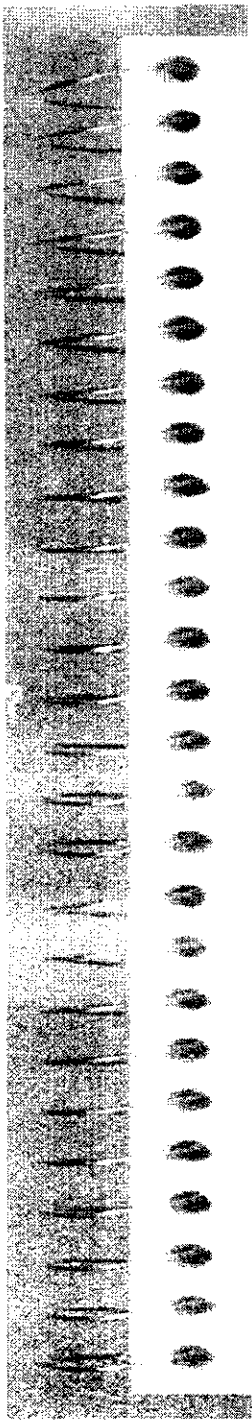
$$\begin{cases} \frac{1}{x_1} \frac{dx_1}{dt} = B_1 - D_1 = f_1(x_1, x_2) \\ \frac{1}{x_2} \frac{dx_2}{dt} = B_2 - D_2 = f_2(x_1, x_2) \end{cases}$$

Definition of two-species interactions

	$\frac{\partial f_1}{\partial x_2}$	$\frac{\partial f_2}{\partial x_1}$
Predation	-	+
Competition	-	-
Cooperation	+	+

$\frac{\partial f_i}{\partial x_j} \equiv$ Interspecific interactions

$\frac{\partial f_i}{\partial x_i} \equiv$ Intraespecific interactions

- 
- If $f_i \in C^1$, then the system has unique solutions to initial value problems.
 - Since $x_i' = x_i f_i(x_1, x_2)$ once the solution is on one axis, it stays in that axis.
 - \mathbb{R}_+^2 is invariant (trajectories do not cross the axis).

Lotka-Volterra Systems

$$f_i(x_1, x_2) = a_i + b_{1i}x_1 + b_{2i}x_2$$

ω Predation

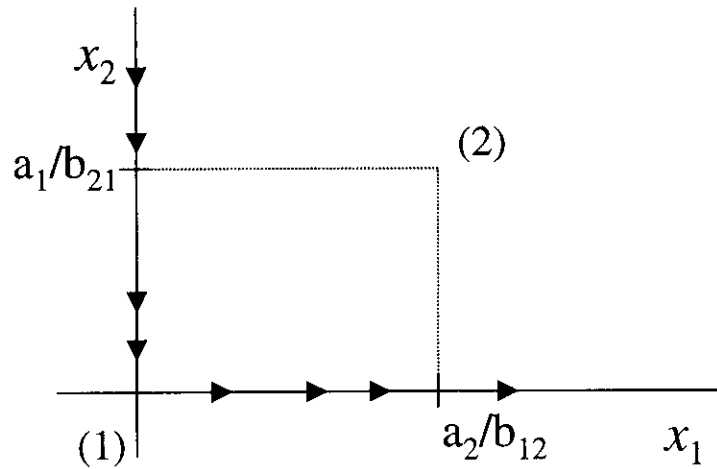
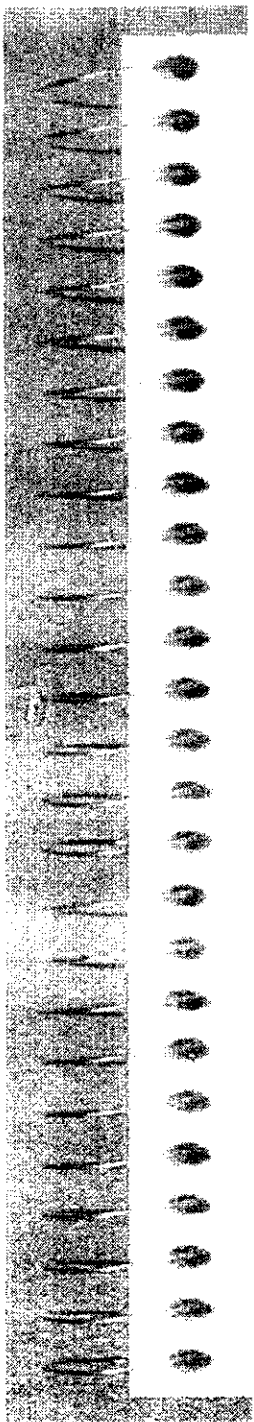
$$\begin{cases} \frac{dx_1}{dt} = x_1(a_1 - b_{21}x_2) \\ \frac{dx_2}{dt} = x_2(-a_2 + b_{12}x_1) \end{cases}$$

No density dependence \Rightarrow no terms in x_i^2

Equilibria

(1) $(x_1, x_2) = (0, 0)$

(2) $(x_1, x_2) = \left(\frac{a_2}{b_{12}}, \frac{a_1}{b_{21}} \right)$



(1) is instable

(2) is a center

Linearization about point (2)

$$\begin{vmatrix} \frac{\partial f_1}{\partial x_1} \Big|_{x^*} - \lambda & \frac{\partial f_1}{\partial x_2} \Big|_{x^*} \\ \frac{\partial f_2}{\partial x_1} \Big|_{x^*} & \frac{\partial f_2}{\partial x_2} \Big|_{x^*} - \lambda \end{vmatrix} = \lambda^2 + b_{12}b_{21} \quad \Rightarrow \quad \lambda = \pm i\sqrt{b_{12}b_{21}}$$

no conclusion from linearization

Consider $\frac{dx_1}{dt} = \frac{dx_1}{dx_2} = \frac{x_1(a_1 - b_{21}x_2)}{x_2(-a_2 + b_{12}x_1)}$

Separation of variables

$$\frac{(-a_2 + b_{12}x_1)}{x_1} dx_1 = \frac{(-a_1 + b_{21}x_2)}{x_2} dx_2$$

$$\Rightarrow \text{solutions satisfy } \frac{x_2^{a_1} x_1^{a_2}}{e^{b_{21}x_2} e^{b_{12}x_1}} = \text{constant}$$

These are simple closed curves that contain

the equilibrium $\left(\frac{a_2}{b_{12}}, \frac{a_1}{b_{21}} \right)$ in their interior

The Story

Umberto D'Ancona Biologist

Vito Volterra Mathematician and father in law

Port of Fiume, Adriatic Sea

Percentage of selachians
(sharks, rays, skates)
versus good fish in the fishery

<u>Year</u>	<u>%</u>	
1914	11.9	
1915	21.4	} World War I
1916	22.1	
1917	21.2	
1918	36.4	
1919	27.3	
1920	16.0	
1921	15.9	
1922	14.8	
1923	10.7	

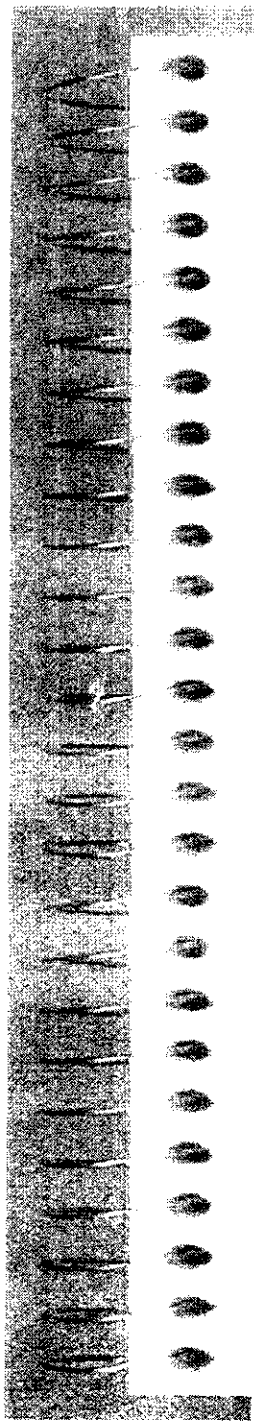
D'Ancona's Questions

- During the war less harvesting was done.
Does this produce an increase in selachians?
- Why does a reduced level of harvesting favor the predators more than the prey?

Volterra's Reasoning

- Consider a fish population $x(t)$
and a predator population $y(t)$
- Food fish do not compete intensively for their food supply:
plankton is abundant and fish population not very dense
- In the absence of selanchias, food fish would grow according to the Malthusian law

$$x' = a x, \quad a > 0$$



- Number of contacts per unit time between predators and prey is

$$b x y, \quad b > 0$$

- Hence $x' = a x - b x y$
- Predators have a natural rate of decrease $-c y, \quad c > 0$
and they increase at rate $d x y, \quad d > 0$
proportional to their food supply.

- Thus $y' = -c y + d x y$

- Without fishing effects the model is

$$\begin{cases} x' = ax - bxy \\ y' = -cy + dxy \end{cases}$$

- Without fishing, steady states are

$$(1) \quad (0, 0)$$

$$(2) \quad \boxed{\left(\frac{c}{d}, \frac{a}{b} \right)}$$

- Including fishing

Fishing decreases both populations at the same rate ∂

$$\begin{cases} x' = ax - bxy - \varepsilon x = (a - \varepsilon)x - bxy \\ y' = -cy + dxy - \varepsilon y = -(c + \varepsilon)y + dxy \end{cases}$$

This means that the steady states are

$$(1) \quad (0, 0)$$

$$(2) \quad \boxed{\left(\frac{c + \varepsilon}{d}, \frac{a - \varepsilon}{b} \right)}$$

following approximate laws:

(1) Small fluctuations are isochronous, i.e. their period is not visibly affected either by the initial

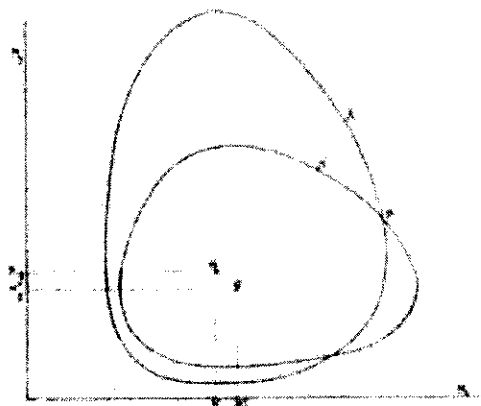


FIG. 1.

number of individuals, or by the conditions of protection and offence.

(2) The period of fluctuation is proportional to the product of the square roots of the time required for the first species to double itself, and for the second species to reduce itself to half. If the first species doubles itself in the time t_1 and the second species is reduced to half

in the time t_2 , the period is $T = \frac{2\pi}{\log_2 2} \sqrt{t_1 t_2} = 0.69 \sqrt{t_1 t_2}$.

(3) The steady destruction of individuals of the eating species accelerates the fluctuation, and the destruction of individuals of the eaten species retards it.

With the contemporaneous and uniform destruction of individuals of the two species, the ratio between the amplitude of the fluctuation of the eaten species and that of the eating species tends to increase.

In Fig. 1 are represented two cycles, the second of which corresponds to a perturbation produced in the first by a constant and proportionate destruction of the individuals of the two species. The centre Q of the perturbed curve is displaced, in respect to the centre O of the primitive curve, downwards and to the right; this reveals an augmentation of the average number of individuals of the first species, and a diminution of the average number of the second.

Law III is undoubtedly the most interesting of all, because it affords the best actual verification as far found of the theory. For Dr. U. d'Ancona, comparing fishery statistics in the Adriatic Sea before the War, during the War (when fishing almost ceased), and after fishing was resumed at the end of the War, has ascertained that the voracious species (selachians), which fed on other fishes, had increased during the War as compared with the preceding and following periods, while the contrary had been the case for the

to prey, were worse off than before. This is in agreement with Fig. 1, and with Law III. My theoretical researches, which I was induced to undertake by the statistical studies begun by Dr. d'Ancona, correspond accordingly with his results.

Charles Darwin had an intuition of these phenomena in relation to the struggle for existence when in Chap. III of his "Origin of Species" he writes: "The amount of food for each species of course gives the extreme limit to which each can increase, but very frequently it is not the obtaining food, but the serving as prey to other animals, which determines the average number of a species. Thus there seems to be little doubt that the stock of partridges, grouse, and hares on any very large estate depends chiefly on the destruction of vermin. If not one head of game were shot during the next twenty years in England, and at the same time if no vermin were destroyed, there would in all probability be less game than at present, although hundreds of thousands of game animals are now annually shot."

Law III is, however, true only up to a certain limit. It is evident that if the destruction of both species continue, their exhaustion will ensue. It is therefore necessary to ascertain up to just what point it is profitable to destroy both species in order to obtain the greatest augmentation in the average number of the eaten species. We arrive in this manner at a curious example of a mathematical *upper bound* without the existence of a *survival limit*. There is in fact a limit of destruction beyond which both species are exhausted. If we remain below it, the average number of the eaten species grows as this limit is approached, but once the limit is reached, the eating species tends to exhaustion and the fluctuation ceases, while the number of individuals of the eaten species tends asymptotically

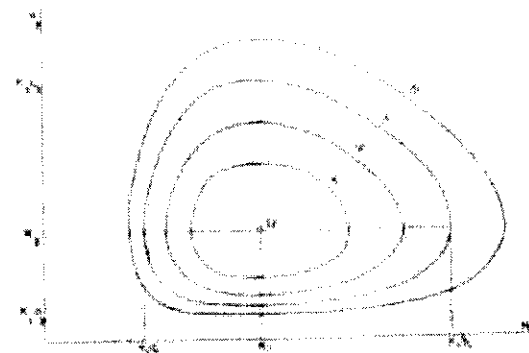


FIG. 2.

towards a value which is less than the average formerly reached.

Besides the case dealt with above, a study of variations in the number of individuals of two associated



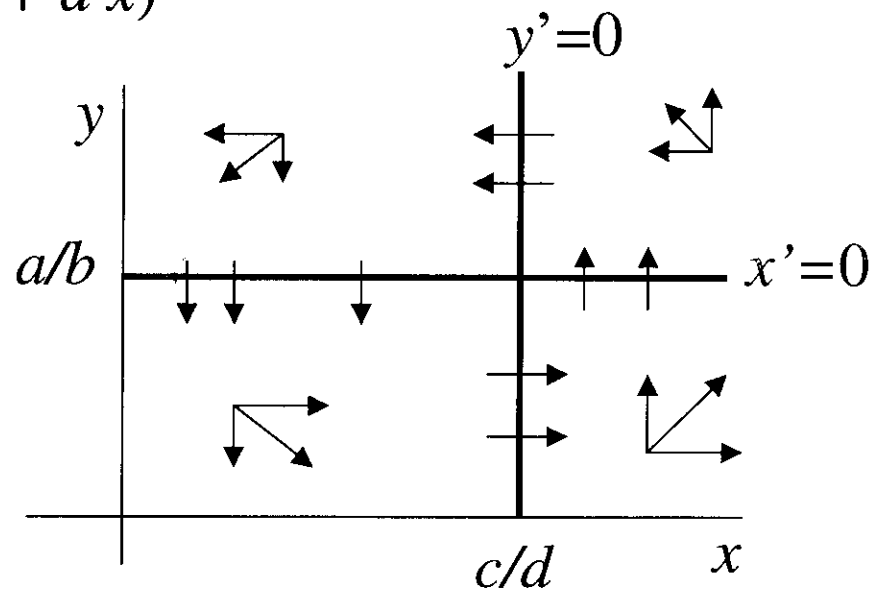
Interpretation

D'Ancona's data are averages over
one year periods

Method of Isoclines

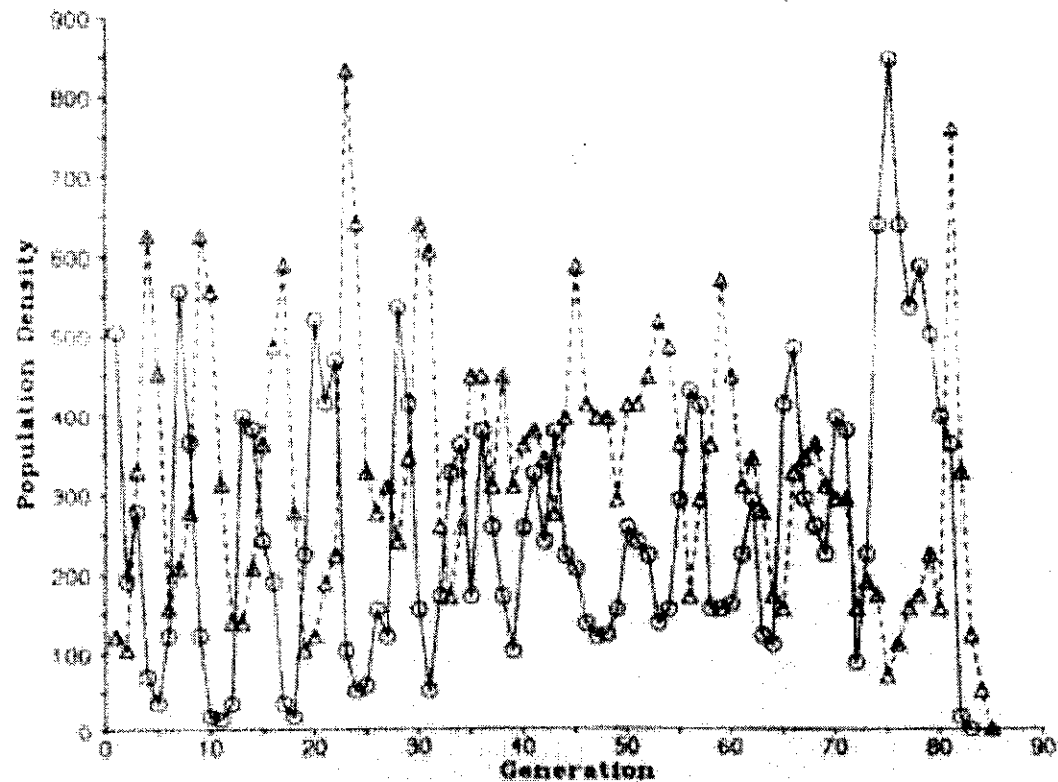
$$x' = x(a - by)$$

$$y' = y(-c + dx)$$



Fluctuations in population density in a host-parasite system

Figure 6.2. Fluctuations in population density in a host-parasite system of the azuki bean weevil (*Callosobruchus chinensis* - ○) (host) and its larval wasp parasite (*Heterospilus prosopidis* - △) (redrawn from Utida, 1957).



More General Predator-Prey Models

Harrison (1979) discussed the global asymptotic stability of an equilibrium of the model:

$$\frac{dx}{dt} = a(x) - f(x)b(x)$$

$$\frac{dy}{dt} = n(x)g(y) + c(y) \quad \text{where } f \text{ and } g \text{ are positive on } \mathbb{R}_+$$

$a(x)$ growth rate due to all factors except predation,

$c(y)$ rate of change in predator population.

$N(x)$, $b(y)$ are non decreasing functions such that

$f(x) b(y)$ is the functional response of the predator,

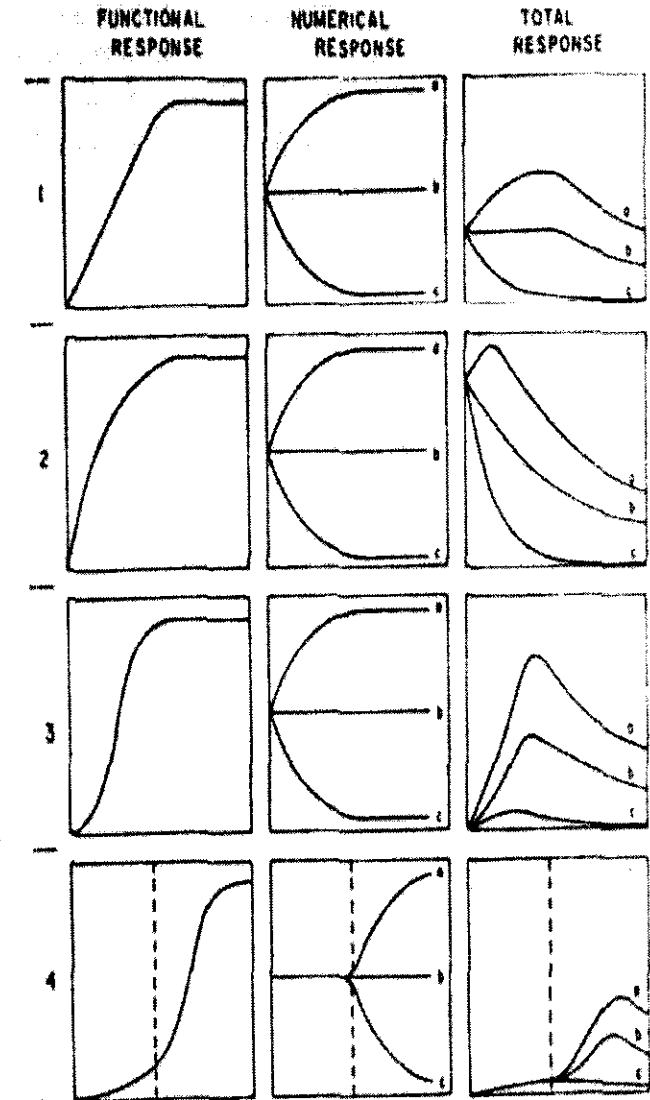
$n(x) g(y)$ is the numerical response of the predator.

Functional Response

Type I (linear): $\varphi(x) = \alpha x$

Type II (hiperbolic): $\varphi(x) = \frac{\alpha x}{k + x}$

Type III (sigmoid): $\varphi(x) = \frac{\alpha x^2}{k^2 + x^2}$





Example

The Lotka -Volterra predator-prey system

$$\frac{dx_1}{dt} = x_1(a_1 - b_{11}x_1 - b_{12}x_2)$$

$$\frac{dx_2}{dt} = x_2(-a_2 + b_{21}x_1)$$

Satisfies the conditions of the theorem, so the equilibrium

$\left(\frac{a_2}{b_{21}}, \frac{a_1 b_{21} - b_{11} a_2}{b_{21} b_{12}} \right)$ is globally asymptotically stable.

The global asymptotic stability of this model should be contrasted with the neutrally stable cycles of the Volterra model.

Do Predator -Prey systems approach equilibria or cycle?

Prey-Predator	Location	Apparent dynamics
sparrow-hawk	Europe	Equilibrium
muskrat-mink	Central N. America	Equilibrium
hare-lynx	Boreal N. America	Cyclic
mule deer-mountain lion	Rocky Mountains	Equilibrium
white-tailed deer-wolf	Ontario	Equilibrium
moose-wolf	Isle Royale	Equilibrium
caribou-wolf	Alaska	Equilibrium
white sheep-wolf	Alaska	Equilibrium

Tanner, 1975

Stable limit cycle \Leftrightarrow intrinsic growth rate r of prey exceeds that of its predators.

May (1976):

Prey with high r plus a large K is necessary for cycles.

Competition

Lotka - Volterra - Gause Models

Gause (1934) developed a theory of competition based on experimental work

$$\frac{dx_1}{dt} = x_1(a_1 - b_1x_1 - b_{12}x_2)$$

$$\frac{dx_2}{dt} = x_2(a_2 - b_2x_2 - b_{21}x_1)$$

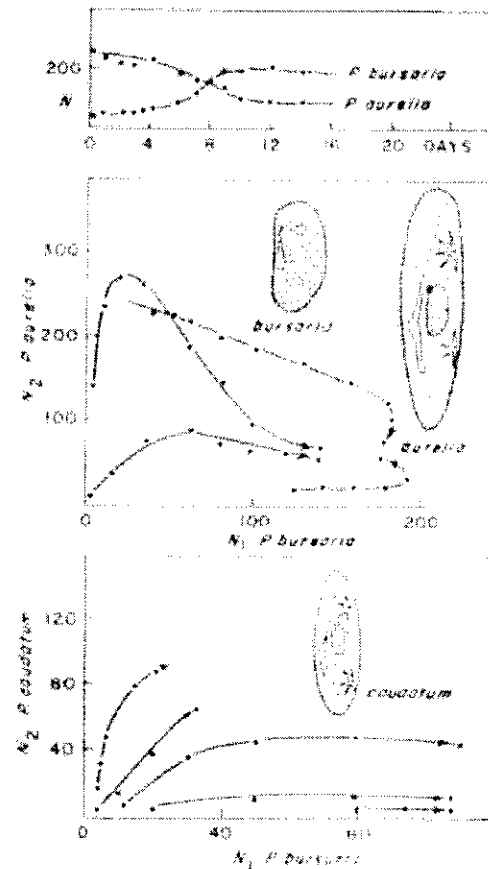


FIGURE 30. Upper panel, population of *Paramecium aurelia* and of *P. bursaria* introduced into the *P. aurelia* culture. Middle panel, trajectories converging on a stable point when *P. aurelia* and *P. bursaria* are cultivated together. Bottom panel, trajectories when *P. caudatum*, much more sensitive to metabolic products, is cultivated with *P. aurelia* (Gause, modified).

There are four ecologically feasible outcomes:

(a) The two populations can coexist:

⇒ unique positive equilibrium is

globally asymptotically stable $x_1 \leftrightarrow x_2$

(b) The winner of the competition depends upon initial conditions:

⇒ hiperbolic (saddle) point: $x_1 \leftrightarrow x_2$

(c) One population survives, the other goes to extinction

⇒ $x_1 \gg x_2$ or $x_2 \gg x_1$

Outcomes of Competition

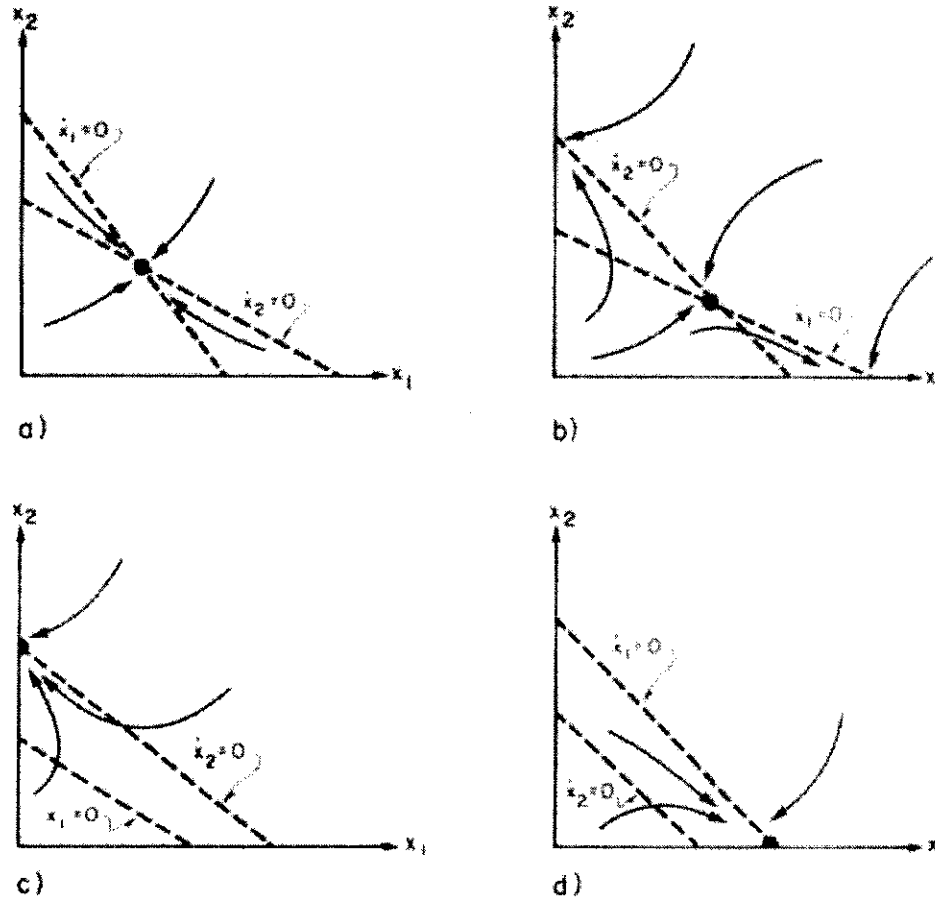


Fig. 3.1a-d. Outcomes of competition as determined by a Lotka-Volterra model. **a** $x_1 < x_2$, **b** $x_1 > x_2$, **c** $x_2 > x_1$, **d** $x_1 > x_2$. See text for details

Models of Cooperation

Obligatory association:

survival of each species depends upon
the presence of the other.

Facultative association:

not obligatory

Lotka - Volterra models of facultative association

$$\begin{cases} \frac{dx_1}{dt} = x_1 (a_1 - b_1 x_1 + c_{12} x_2) \\ \frac{dx_2}{dt} = x_2 (a_2 - b_2 x_2 + c_{21} x_1) \end{cases}$$

all constants being positive.

Behavior:

- $b_1 b_2 - c_{12} c_{21} > 0 \Rightarrow$ positive globally asymptotically stable equilibrium
- $b_1 b_2 - c_{12} c_{21} \leq 0 \Rightarrow$ unbounded growth for each component

Lotka - Volterra models for obligatory interactions

- Each population will decay exponentially in the absence of the other species
- Interactions are represented by mass action formulations

$$\frac{dx_1}{dt} = x_1(-a_1 + b_1x_2)$$

$$\frac{dx_2}{dt} = x_2(-a_2 + b_2x_1)$$

These models can exhibit an orgy of mutuality:

It can be shown that $\exists T < \infty$ such that

$$\lim_{t \rightarrow T} x_1(t) = \infty \quad \text{or} \quad \lim_{t \rightarrow T} x_2(t) = \infty$$

Phase-plane diagram of an obligatory cooperation model

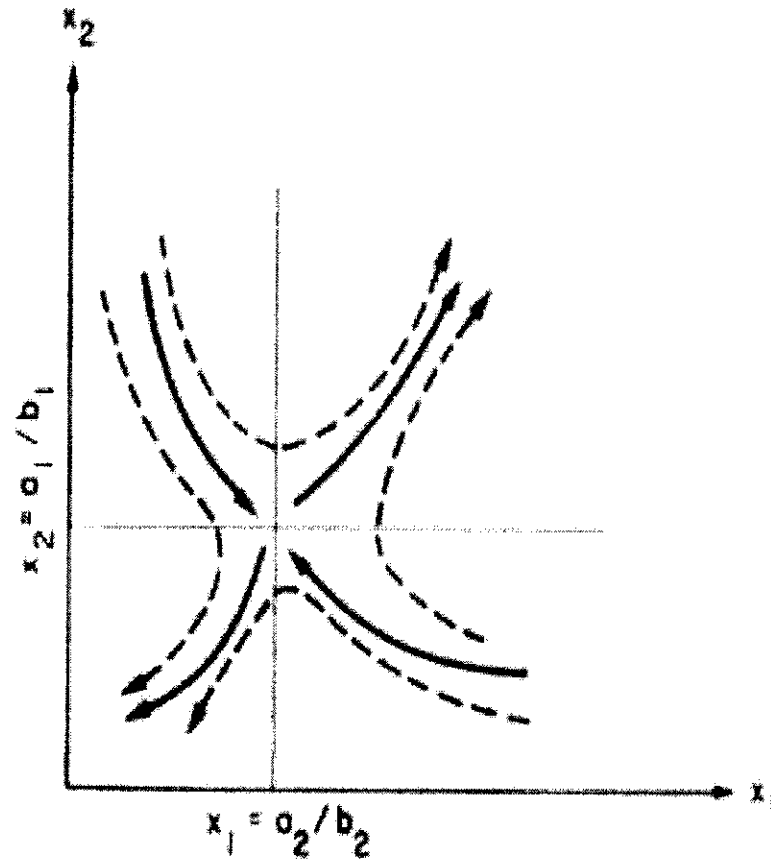


Fig. 4.1. Phase plane diagram of a Lotka-Volterra model of obligatory cooperation

Multiple-species Communities

More generally, a system comprised of k species with populations x_1, x_2, \dots, x_k would be governed by k equations

$$\frac{dx_1}{dt} = f_1(x_1, \dots, x_k)$$

$$\frac{dx_2}{dt} = f_2(x_1, \dots, x_k)$$

\vdots

$$\frac{dx_k}{dt} = f_k(x_1, \dots, x_k)$$

Or in vector notation

$$\frac{dX}{dt} = F(X)$$

Suppose we can solve $F(X) = 0$
so as to identify steady-state points

$$X^* = (x_1^*, x_2^*, \dots, x_k^*).$$

In linearizing the equation $\frac{dX}{dt} = F(X)$

we find the Jacobian of $F(X)$:

$$J = \frac{\partial F}{\partial X} \Big|_{X^*} = \begin{pmatrix} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} & \dots & \frac{\partial f_1}{\partial x_k} \\ \vdots & \vdots & & \vdots \\ \vdots & \vdots & & \vdots \\ \frac{\partial f_k}{\partial x_1} & \frac{\partial f_k}{\partial x_2} & \dots & \frac{\partial f_k}{\partial x_k} \end{pmatrix}_{X^*}$$

In population ecology, this is usually called the community matrix.

The eigenvalues of this $k \times k$ matrix satisfy

$$\det(J - \lambda I) = 0,$$

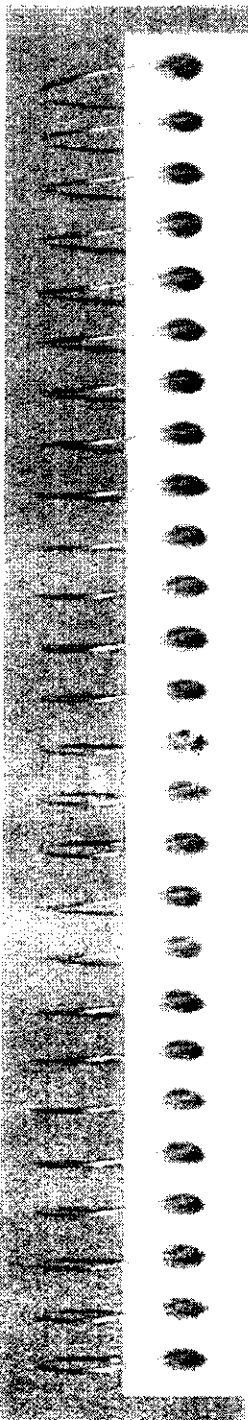
or more specifically

$$\lambda^k + a_1 \lambda^{k-1} + a_2 \lambda^{k-2} + \dots + a_k = 0$$

Even when we cannot compute all the eigenvalues, we can obtain information about the system.

Let $\lambda_1, \lambda_2, \dots, \lambda_k$ be all the eigenvalues of the linearized system

$$\frac{dX}{dt} = J.X$$



Close to the steady state X^* , each species population can be represented as

$$x_i = x_i^* + \alpha_1 e^{\lambda_1 t} + \alpha_2 e^{\lambda_2 t} + \dots + \alpha_k e^{\lambda_k t}$$

- If $\text{Re } \lambda_j > 0$, then $x_i - x_i^*$ is an increasing function of t
 $\Rightarrow x_i$ will not return to the equilibrium x_i^*

Thus the stability of a steady state can be settled if we can determine whether or not all eigenvalues have negative real parts

The Routh-Hurwitz Criteria

Given the characteristic equation

$$\lambda^k + a_1\lambda^{k-1} + a_2\lambda^{k-2} + \dots + a_k = 0$$

we can define the matrices

$$H_1 = (a_1), \quad H_2 = \begin{pmatrix} a_1 & 1 \\ a_3 & a_2 \end{pmatrix}, \quad H_3 = \begin{pmatrix} a_1 & 1 & 0 \\ a_3 & a_2 & a_1 \\ a_5 & a_4 & a_3 \end{pmatrix}, \quad \dots$$

$$H_j = \begin{pmatrix} a_1 & 1 & 0 & 0 & \dots & 0 \\ a_3 & a_2 & a_1 & 1 & & 0 \\ \vdots & & & & & \\ a_{2j-1} & a_{2j-2} & a_{2j-3} & a_{2j-4} & & a_j \end{pmatrix}$$

where the term (l, m) in H_j is

$$a_{lm} = \begin{cases} a_{2l-m} & \text{for } 0 < 2l - m < k \\ 1 & \text{for } 2l = m \\ 0 & \text{for } 2l < m \text{ or } 2l > k + m \end{cases}$$

Criteria:

The steady state X^* is stable if and only if
 $\det H_j > 0$ for $j=1, 2, \dots, k$

The conditions are

For

$$k=2: a_1 > 0, a_2 > 0$$

$$k=3: a_1 > 0, a_3 > 0, a_1 a_2 > a_3$$

$$k=4: a_1 > 0, a_3 > 0, a_4 > 0, a_1 a_2 a_3 > a_3^2 + a_1^2 a_4$$

Example

Consider the system where x is a predator and y and z are its prey.

$$\frac{dx}{dt} = \alpha(xz) + \beta(xy) - \gamma x$$

$$\frac{dy}{dt} = \delta y - \varepsilon (xy)$$

$$\frac{dz}{dt} = \mu z(\eta - z) - \chi (xz)$$

Steady states:

$$x^* = \frac{\delta}{\varepsilon}$$

$$y^* = \gamma - \alpha z^*$$

$$z^* = v - \frac{\chi}{\mu} x^*$$

Makes sense when $\gamma > \alpha z^*$ and $v > \frac{\chi}{\mu} x^*$

The jacobian matrix is

$$J = \begin{pmatrix} 0 & \beta x^* & \alpha x^* \\ -\varepsilon y^* & 0 & 0 \\ -\chi z^* & 0 & -\mu z^* \end{pmatrix}$$

The characteristic equation is

$$\lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3 = 0$$

where

$$a_1 = \mu z^*$$

$$a_2 = \varepsilon \beta x^* y^* + \chi \alpha x^* z^*$$

$$a_3 = \mu \varepsilon \beta x^* y^* z^*$$

The conditions are:

$$a_1 > 0$$

$$a_2 > 0$$

$$a_1 a_2 > a_3$$

The first two hold true.

It is easy to verify the third since

$$a_1 a_2 = \mu z^* (\epsilon \beta x^* y^* + \chi \alpha x^* z^*) > \mu \epsilon \beta x^* y^* z^* = a_3$$

We can conclude that the steady state is a stable one