Lecture 15
Lotka-Volterra.

Shlomo Sternberg

April 14 - 21, 2009

The Lotka - Volterra predator prey equations were discovered independently by Alfred Lotka and by Vito Volterra in 1925-26. These equations have given rise to a vast literature, some of which we will sample in this lecture.

Here is how Volterra got to these equations: The number of predatory fishes immediately after WWI was much larger than before the war. The question as to why this was so was posed to the mathematician Volterra by his prospective son-in-law Ancona who was a marine biologist.

Much of the more recent results (in the second part of this lecture) are taken from the book *Evolutionary Games and Population Dynamics* by Josef Hofbauer and Karl Sigmund.

For a discussion of some of these issues at a level requiring less mathematics that we require in these lectures (and hence without some of the proofs) see the book *Evolutionary Dynamics* by Martin Nowak.

The L-V equations.

Here is Volterra's solution to the problem: Let x denote the density of prey fish and y denote the density of predator fish. Assume the equations

$$\begin{aligned} \dot{x} &= x(a - by) \\ \dot{y} &= y(-c + dx) \end{aligned} \tag{1}$$

where

$$a, b, c, d > 0.$$

$$\begin{aligned}\dot{x} &= x(a - by)\\ \dot{y} &= y(-c + dx)\end{aligned}$$

The idea of the first equation is that in the absence of predators, the prey would grow at a constant rate a, but decreases linearly as a function of the density y of the predators. Similarly, in the absence of prey, the density of predators would decrease but the rate increases proportional to the density of the prey.

We are interested in solutions to these differential equations in the first quadrant

$$\mathbb{R}^2_+ = \{(x, y) | x \geq 0, y \geq 0\}.$$

The zeros of the vector field.

$$\begin{aligned}\dot{x} &= x(a-by)\\ \dot{y} &= y(-c+dx)\end{aligned}$$

The null-clines (where either $\dot{x}=0$ or $\dot{y}=0$ are zero) are the coordinate axes and the lines $y=a/b$ and $x=c/d$. The first quadrant is invariant . The origin is a saddle point.

$$\begin{aligned} \dot{x} &= x(a - by) \\ \dot{y} &= y(-c + dx) \end{aligned}$$

The other point where the right hand side is zero is

$$\begin{pmatrix} \overline{x} \\ \overline{y} \end{pmatrix} := \begin{pmatrix} \frac{c}{d} \\ \frac{a}{b} \end{pmatrix}$$

where the linearized equation has matrix

$$\begin{pmatrix} 0 & -bc/d \\ da/b & 0 \end{pmatrix}$$

with purely imaginary eigenvalues $\pm i\sqrt{ac}$.

$$\begin{aligned}\dot{x} &= x(a-by)\\ \dot{y} &= y(-c+dx)\end{aligned}$$

If we multiply the first equation by $(c-dx)/x$ and the second by $(a-by)/y$ and add we get

$$\left(\frac{c}{x}-d\right)\dot{x}+\left(\frac{a}{y}-b\right)\dot{y}=0$$

or

$$\frac{d}{dt}[c\log x - dx + a\log y - by] = 0.$$

Let

$$H(x) := \overline{x}\log x - x, \quad G(y) := \overline{y}\log y - y,$$

and

$$V(x,y) := dH(x) + bG(y).$$

Then V is constant on flow lines.

All trajectories in the interior of the quadrant are periodic.

$$H(x) := \overline{x}\log x - x, \quad G(y) := \overline{y}\log y - y,$$

and

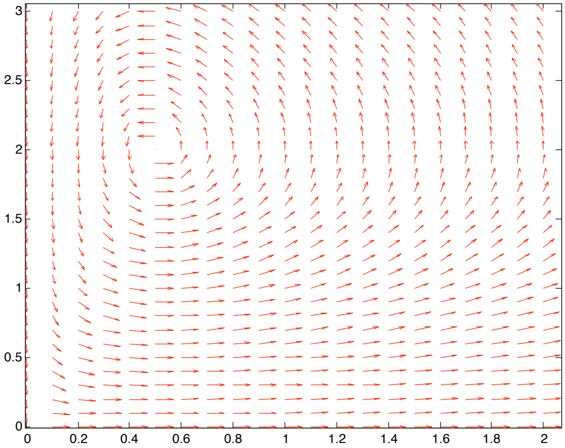
$$V(x,y) := dH(x) + bG(y).$$

Then V is constant on flow lines. Since

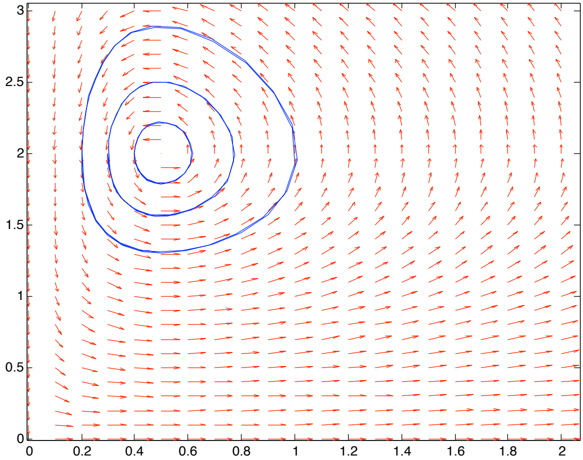
$$\frac{dH}{dx} = \frac{\overline{x}}{x} - 1, \quad \frac{d^2H}{dx^2} = -\frac{\overline{x}}{x^2} < 0$$

we see that H achieves a maximum at $\overline{x}$ and similarly G assumes a maximum at $\overline{y}$. Thus V has a unique maximum in the interior of the quadrant at the critical point. Thus the level curves of V, which are solution curves, are closed curves: all trajectories are periodic.

LV vector field with a=2, b=1, c=.25,d=1.



Some trajectories.



The fixed point as an average.

Suppose we are on a trajectory of period T, so $x(T) = x(0)$. From

$$\frac{d}{dt}\log x = \frac{\dot{x}}{x} = a - by$$

it follows by integration that

$$0 = \log x(T) - \log x(0) = aT - b\int_0^T y(t)dt$$

or

$$\frac{1}{T}\int_0^T y(t)dt = \overline{y}$$

and similarly

$$\frac{1}{T}\int_0^T x(t)dt = \overline{x}.$$

Volterra's explanation of why fishing decreases the number of predators.

Fishing reduces the rate of increase of the prey, so a is replaced by $a - k$ and increases the rate of decrease of the predator, so c is replaced by $c + m$, but does not change b or d - the interaction coefficients. So a/b is replaced by $(a - k)/b$ - the average number of predators is decreased by fishing and the average number of prey is increased. Stoppage of fishing increases the average number of predators and decreases average the number of prey.

A moral lesson.

If the prey are "pests" and the predators are their natural enemies, applying non-specific insecticides may actually increase the pest population.

A more realistic model.

Suppose we make the equations more realistic by adding self competition terms and so get the equations

$$\begin{aligned} \dot{x} &= x(a - ex - by) \\ \dot{y} &= y(-c + dx - fy) \end{aligned} \tag{2}$$

where

$$a, b, c, d, e, f > 0.$$

The first quadrant is still invariant, and there is an equilibrium point on the x-axis at $x = a/e$. There is no equilibrium point on the positive y-axis. The null-clines are now the axes and the two lines

$$ex + by = a, \quad \text{and} \quad dx - fy = c$$

the first with negative slope and the second with positive slope.

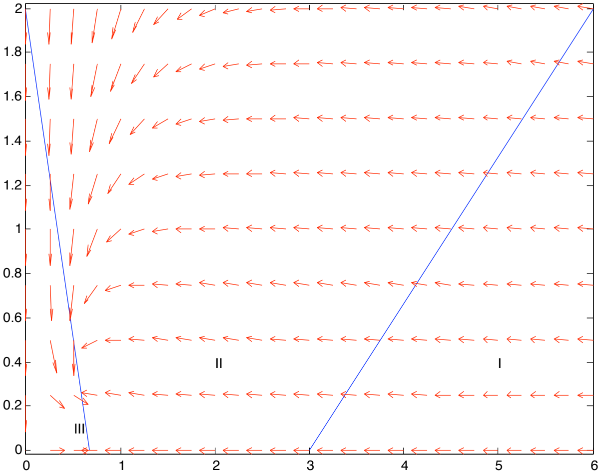
The null-clines are now the axes and the two lines

$$ex + by = a, \quad \text{and} \quad dx - fy = c$$

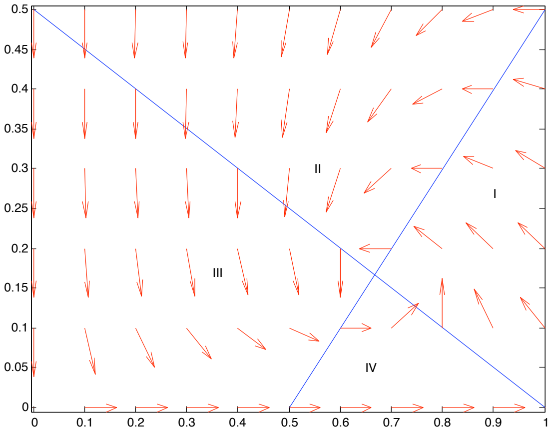
the first with negative slope and the second with positive slope.

All hinges on whether or not they intersect in the first quadrant. If they don't, the quadrant is divided into three regions: in the region I to the right of the line $\dot{y} = 0$ of positive slope, we have $\dot{x} < 0$ so a trajectory starting in this region moves to the left, entering region II. It keeps moving to the left until it crosses the line $\dot{x} = 0$, entering region III, where it points down and to the right and heads toward the fixed point on the x-axis. The predators become extinct.

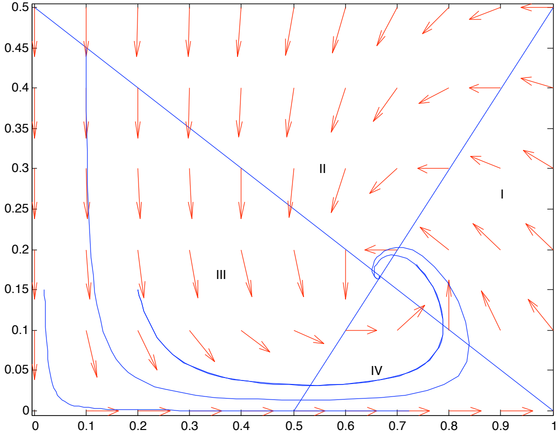
The predators become extinct.



The second alternative is that the lines intersect in the first quadrant, dividing it into four regions:



Some trajectories from ode45.



It looks as if trajectories (except those on the axes) are spiraling in to the zero of the vector field. Let's prove this: Label the fixed point as

$$\begin{pmatrix} \overline{x} \\ \overline{y} \end{pmatrix}.$$

With the same H, G and V as before, namely

$$H(x) := \overline{x}\log x - x, \quad G(y) := \overline{y}\log y - y,$$

and

$$V(x,y) := dH(x) + bG(y)$$

we have

$$\dot{V} = \frac{\partial V}{\partial x}\dot{x} + \frac{\partial V}{\partial y}\dot{y}$$

$$= d(\frac{\overline{x}}{x} - 1)x(a - by - ex) + b(\frac{\overline{y}}{y} - 1)y(-c + dx - fy).$$

$$\dot{V} = d(\frac{\overline{x}}{x} - 1)x(a - by - ex) + b(\frac{\overline{y}}{y} - 1)y(-c + dx - fy).$$

Write $a = e\overline{x} + b\overline{y}$ and $c = d\overline{x} - f\overline{y}$. We get

$$d(\overline{x} - x)(b\overline{y} + e\overline{x} - by - ex) + b(\overline{y} - y)(-d\overline{x} + f\overline{y} + dx - fy)$$

which simplifies giving

$$\dot{V}(x, y) = de(\overline{x} - x)^2 + bf(\overline{y} - y)^2.$$

This is non-negative, and strictly positive except at the equilibirum point. Hence V is steadily increasing along each orbit, which must then head to the equilibrium point. $\square$

Simple equations of competition.

If x and y denote the density of populations of two species competing for the same resources, then the rates of growth $\dot{x}/x$ and $\dot{y}/y$ will be decreasing functions of both x and y. The simplest assumption is that these decreases be linear which leads to the equations

$$\begin{aligned} \dot{x} &= x(a - bx - cy) \\ \dot{y} &= y(d - ex - fy) \end{aligned}$$

with

$$a, b, c, d, e, f > 0.$$

The null clines.

Again the first quadrant $\mathbb{R}^2_+$ is invariant. The x and y null-clines are given by the lines

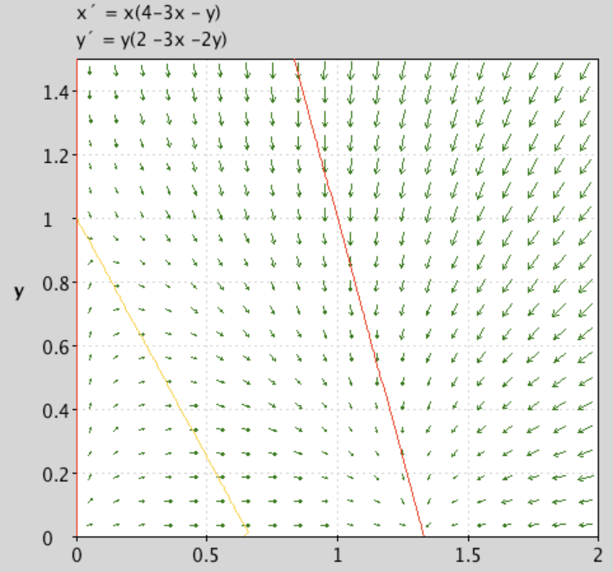
$$\begin{aligned} a - bx - cy &= 0 \\ d - ex - fy &= 0 \end{aligned}$$

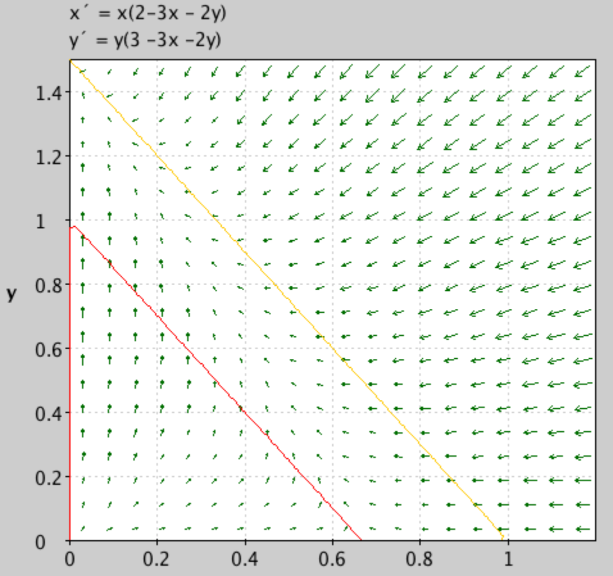
this time both of negative slope.

We will ignore the degenerate case where these lines are parallel. So we are left with two possibilities:

- The point of intersection does not lie in $\mathbb{R}^2_+$.
- The point of intersection does lie in $\mathbb{R}^2_+$.

If point of intersection does not lie in $\mathbb{R}^2$ then one species tends to extinction. The other species is said to be dominant. Here are the two possible cases:


x´ = x(4−3x − y)
y´ = y(2 −3x −2y)
y
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
0.5
1
1.5
2


x´ = x(2–3x – 2y)
y´ = y(3 –3x –2y)
y
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
1

If the two null-clines intersect in $\mathbb{R}^2$ the point of intersection is at

$$\overline{x} = \frac{af - cd}{bf - ce}, \quad \overline{y} = \frac{bd - ae}{bf - ce}$$

The Jacobian matrix at this point is

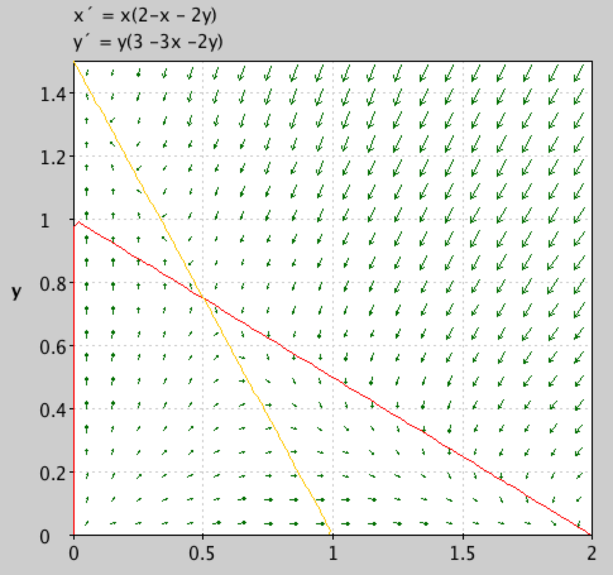
$$J = \begin{pmatrix} -b\overline{x} & - - c\overline{x} \\ -e\overline{y} & -f\overline{y} \end{pmatrix}$$

with determinant

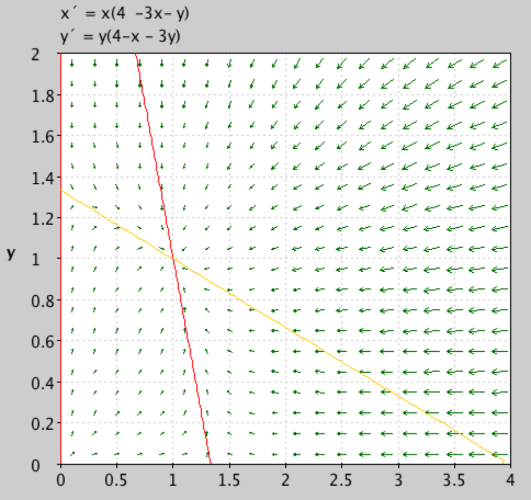
$$det(J) = \overline{xy}(bf - ce).$$

We can have (case 3)- a saddle, or (case 4) a sink.

In case 3 one or the other species dominates depending on the initial conditions:


x´ = x(2−x − 2y)
y´ = y(3 −3x −2y)
y
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0
0.5
1
1.5
2

In case 4 all trajectories lead to the stable fixed point of "equilibrium co-existence".



In two dimensions, because of Poincaré-Bendixon, we can get more or less complete answers to the global behavior of flows.
We will now embark on the study of the higher dimensional version of the Lotka-Volterra equations where the answers are far less complete.
But we can say something.

A theorem of Liapounov.

We will use a theorem of Liapounov describing the ω-limit set in the presence of a "Liapounov function".

Theorem

Let X be a vector field on some open set $O \subset \mathbb{R}^n$. Let $V : O \to \mathbb{R}$ be a continuously differentiable function. Let $t \mapsto x(t)$ be a trajectory of X. If the derivative $\dot{V}$ of the map $t \mapsto V(x(t))$ satisfies $\dot{V} \geq 0$ (for all t) then $\omega(x) \cap O$ is contained in the set where $XV = 0$.

Remark.

Along $x(t)$ we have $\dot{V}(t) = X(x(t))V$.

Proof of Liapounov's theorem.

If $y \in \omega(x) \cap O$, there is a sequence $t_k \to \infty$ with $x(t_k) \to y$. Hence, by continuity, $(XV)(y) \geq 0$. If XV does not vanish at y, then $(XV)(y) > 0$ and we must show that this can not happen.

If $(XV)(y) > 0$, then for small positive values of t we would have $V(y(t)) > V(y)$. Now by hypothesis $V(x(s))$ is a monotone increasing function of s, and since $x(t_k) \to y$ and $t_k \to \infty$, for any s and sufficiently large k we have

$$V(x(s)) \leq V(x(t_k)) \to V(y).$$

So

$$V(x(s)) \leq V(y)$$

for all s.

Proof of Liapounov's theorem, completed.

$$V(x(s)) \leq V(y) \text{ for all } s.$$

Since $x(t_k) \to y$ we have (for small $t > 0$)

$$x(t_k + t) \to y(t)$$

and hence

$$V(x(t_k + t)) \to V(y(t)) > V(y),$$

a contradiction. $\square$

The Lotka-Volterra equations for n species.

These are

$$\dot{x}_i = x_i\left(r_i + \sum_j a_{ij}x_j\right), \qquad i = 1, \ldots, n.$$

x_i denotes the density of the i-th species, r_i is its intrinsic growth (or decay) rate and the matrix $A = (a_{ij})$ is called the **interaction matrix**.

The positive orthant and its faces are invariant.

$$\dot{x}_i = x_i \left(r_i + \sum_j a_{ij} x_j \right), \qquad i = 1, \ldots, n.$$

If $x_i(0) = 0$, then $x_i(t) \equiv 0$ is a solution of the i-th equation, and hence by the uniqueness theorem of differential equations the only solution. So each of the faces $x_i = 0$ of the positive orthant $\mathbb{R}^n_+$ is invariant under the flow, and hence so is the (interior of) the positive orthant itself.

The vector field given by the right hand side of the equations vanishes when

$$r_i + \sum_j a_{ij} x_j = 0$$

and so zeros of the vector field in the positive orthant correspond to solutions of these equations with all $x_i > 0$.

An interior α or ω point implies a solution of $r_i + \sum_j a_{ij}x_j = 0$ with all positive entries.

To prove this, it is enough to show that if there is no solution to the above equation, then there is a "Liapounov function" V with $XV > 0$ everywhere, since Liapounov's theorem tells us that at any interior ω point we must have $XV = 0$ (and similarly for α points). To construct V, let L be the map $Lx = y$ where

$$y_i = r_i x_i + \sum_j a_{ij} x_j.$$

The image of the positive orthant is some convex cone C. The assumption is that C does not contain the origin.

L is the map $x \mapsto y, \quad y_i = r_i x_i + \sum_j a_{ij} x_j$. The image of the positive orthant is some convex cone C. The assumption is that C does not contain the origin. Since C is convex, there is a hyperplane separating it from the origin. Put another way, there is a vector c such that $c \cdot y > 0$ for all $y \in C$. Now define

$$V(x) := \sum_i c_i \log x_i$$

for all x in the positive orthant. Then

$$\dot{V} = \sum c_i \frac{\dot{x}_i}{x_i} = \sum c_i y_i > 0$$

at all points, proving our claim.

In particular, if there is a periodic solution in the positive orthant, there must also be a fixed point.

Food chains.

A food chain is a system where the first species is prey for the second, the second is prey for the third , etc. up to the n-th which is at the top of the pyramid. Taking competition within each species into account, the differential equations are:

The food chain equations.

$$\begin{aligned}
\dot{x}_1 &= x_1(r_1 - a_{11}x_1 - a_{12}x_2) \\
\dot{x}_2 &= x_2(-r_2 + a_{21}x_1 - a_{22}x_2 - a_{23}x_3) \\
\vdots &\ \vdots\ \vdots \\
\dot{x}_j &= x_j(-r_j + a_{j,j-1}x_{j-1} - a_{jj}x_j - a_{j,j+1}x_{j+1}) \\
\vdots &\ \vdots\ \vdots \\
\dot{x}_n &= x_n(-r_n + a_{n,n-1}x_{n-1} - a_{nn}x_n)
\end{aligned}$$

with all the r_i and a_{ij} positive.

Theorem

If the food chain equations have an interior rest point

$$p = \begin{pmatrix} p_1 \\ \vdots \\ p_n \end{pmatrix},$$

i.e. a point p where the right hand side of the food chain equations vanish, then p is globally stable in the sense that all orbits in the interior of the positive orthant converge to p.

The proof will consist of constructing a Liapounov function of the form

$$V(x) = \sum c_i(x_i - p_i \log x_i)$$

for suitably chosen constants c_i.

Proof of the food chain theorem, I.

Let $V(x) = \sum c_i(x_i - p_i \log x_i)$. Then

$$\dot{V}(x) = \sum c_i \left(\dot{x}_i - p_i \frac{\dot{x}_i}{x_i}\right).$$

If we write the food chain equations as $\dot{x}_i = x_i w_i$ this becomes

$$\dot{V}(x) = \sum c_i(x_i - p_i)w_i.$$

By assumption, the w_i vanish at p. So, for example,
$r_1 = a_{11}p_1 + a_{22}p_2$ so

$$w_1 = r_1 - a_{11}x_1 - a_{12}x_2 = a_{11}(p_1 - x_1) + a_{12}(p_2 - x_2).$$

Proof of the food chain theorem, II.

$$V(x) = \sum c_i(x_i - p\log x_i), \quad \dot{x}_i = x_i w_i, \quad \dot{V}(x) = \sum c_i(x_i - p_i)w_i.$$

$$\begin{aligned} w_1 &= a_{11}(p_1 - x_1) + a_{12}(p_2 - x_2) \\ w_2 &= a_{21}(x_1 - p_1) - a_{22}(x_2 - p_2) - a_{23}(x_3 - p_3) \\ \vdots \quad &\vdots \quad \vdots \\ w_n &= a_{n,n-1}(x_{n-1} - p_{n-1}) - a_{nn}(x_n - p_n). \end{aligned}$$

So if we set $y_i := x_i - p_i$ we get

$$\dot{V} = -c_1 a_{11} y_1^2 - y_1 y_2 c_1 a_{12} - c_2 a_{22} y_2^2 + c_2 a_{21} y_1 y_2 c_2 - a_{23} y_2 y_3$$
$$-c_3 a_{33} y_3^2 + y_2 y_3 c_3 a_{32} - c_3 a_{34} y_3 y_4 + \cdots$$

Proof of the food chain theorem, III.

$$V(x) = \sum c_i(x_i - p \log x_i), \quad \dot{x}_i = x_i w_i, \quad \dot{V}(x) = \sum c_i(x_i - p_i) w_i.$$

$y_i := x_i - p_i$ Then

$$\dot{V} = -\sum_{j=1}^{n} c_j a_{jj} y_j^2 + \sum_{j=1}^{n-1} y_j y_{j+1}(-c_j a_{j,j+1} + c_{j+1} a_{j+1,j}).$$

Proof of the food chain theorem, completed.

$$\dot{V} = -\sum_{j=1}^{n} c_j a_{jj} y_j^2 + \sum_{j=1}^{n-1} y_j y_{j+1}(-c_j a_{j,j+1} + c_{j+1} a_{j+1,j}).$$

Since all the $a_{j,j+1}$ and $a_{j+1,j}$ are positive, we can choose $c_j > 0$ recursively such that $-c_j a_{j,j+1} + c_{j+1} a_{j+1,j} = 0$, i.e. $c_{j+1}/c_j = a_{j,j+1}/a_{j+1,j}$. Then the second summand above vanishes, and we have

$$\dot{V} = -\sum_{j=1}^{n} c_j a_{jj} y_j^2 \leq 0$$

with strict inequality unless all the $y_i = 0$.

By Liapounov's theorem, the ω limit of every orbit in the interior of the postive orthant is p. $\square$

The replicator equation.

We will let $\overline{S_n}$ denote the simplex consisting of all $x = \begin{pmatrix} x_1 \\ \vdots \\ x_n \end{pmatrix}$ with $x_i \geq 0$ and $\sum_i x_i = 1$. We want to think of a population as being divided into n types $E_1, \dots, E_n$ and of x_i as the frequency of the i-th type E_i. The "fitness" f_i of E_i will be a function of these frequencies, i.e. of x. If the population is very large and the generations blend continuously into each other, we may assume that $x(t)$ is differentiable function of t. The rate of increase of $\dot{x}_i/x_i$ is a measure of the evolutionary success of type E_i. The basic tenet of Darwinism says that we may express this success as the difference between $f_i(x)$ and the average fitness $\overline{f}(x) := \sum x_i f_i(x)$. We obtain the **replicator equation**

$$\dot{x}_i = x_i(f_i(x) - \overline{f}(x)).$$

Elementary properties of the equation $\dot{x}_i = x_i(f_i(x) - \overline{f}(x))$.

If we set $S(x) := x_1 + \cdots + x_n$, then summing the above equations gives the equation

$$\dot{S} = (1 - S)\overline{f}.$$

The (unique) solution of this equation with $S(0) = 1$ is $S(t) \equiv 1$. So the set $\overline{S_n}$ is preserved by the flow. Also, if $x_i(0) = 0$ for some i, then $x_i(t) \equiv 0$. Thus the faces of $\overline{S_n}$ are preserved, and hence so is the open simplex

$$S_n := \{x \in \overline{S_n} | x_i > 0 \ \forall i\}.$$

Linear fitness.

For most of the rest of today's lecture I will assume that the fitnesses are linear functions of x, i.e. there is a matrix A such that $f_i(x) = (Ax)_i$ - the i-th component of Ax. The replicator equations are then cubic equations in x:

$$\dot{x}_i = x_i \left((Ax)_i - x \cdot Ax \right).$$

We shall see that a change of variables will carry the orbits of the replicator equation with linear fitness functions to the orbits of the Lotka-Volterra equations (which are quadratic) in one fewer variables.

These equations are equivalent in the above sense, but some notions are easier to formulate and understand in one setting, and some in the other.

Some preliminaries to the equivalence theorem.

Let us go back temporarily to the general replicator equation

$$\dot{x}_i = x_i(f_i(x) - \overline{f}(x)).$$

If we add a function $h = h(x)$ to all the f_i, this has the effect of replacing $\overline{f}$ by $\overline{f} + h$ since $\sum x_i h = h$ as $\sum x_i = 1$. Thus the right hand side of the above equation is unchanged. So adding a common function to all the f_i does not change the replicator equation.

In case $f_i = (Ax)_i$, if we add a constant c to all the entries in the j-th column of A, this has the effect of adding the function cx_j to all the f_i, so does not change the replicator equation. In particular, this means that (by subtracting off the entry in the last row from each column) we can assume that our matrix A has all entries in the bottom row zero, without changing the replicator equation.

Here is another useful fact about the general replicator equation $\dot{x}_i = x_i(f_i(x) - \overline{f}(x))$. We have

$$\begin{aligned}
\left(\frac{x_i}{x_j}\right)^{\cdot} &= \frac{\dot{x}_i x_j - x_i \dot{x}_j}{x_j^2} \\
&= \frac{(f_i - \overline{f})x_i x_j - (f_j - \overline{f})x_i x_j}{x_j^2} \\
&= \frac{(f_i - f_j)x_i x_j}{x_j^2}
\end{aligned}$$

So

$$\left(\frac{x_i}{x_j}\right)^{\cdot} = \left(\frac{x_i}{x_j}\right)(f_i(x) - f_j(x)).$$

Consider the map of the set $\{y \in \mathbb{R}^n_+ | y_n = 1\}$ onto the set

$$\hat{S}_n := \{x \in \overline{S_n} | x_n > 0\}$$

given by

$$x_i = \frac{y_i}{\sum_j y_j}, \quad i = 1, \ldots, n.$$

The inverse map $x \mapsto y$ is given by

$$y_i = \frac{y_i}{y_n} = \frac{x_i}{x_n}.$$

If x satisfies the general replicator equation then

$$\dot{y}_i = y_i(f_i(x) - f_n(x))$$

by the results of the previous slide.

$$\dot{y}_i = y_i(f_i(x) - f_n(x)).$$

Now suppose that $f_i(x) = (Ax)_i$ and we have chosen the matrix A to have its bottom row all zero (which we can do without changing the equations). Then $f_n(x) \equiv 0$ and the preceding equations become

$$\dot{y}_i = y_i \sum_{j=1}^{n} a_{ij} x_j = y_i \left(\sum_{j=1}^{n-1} a_{ij} y_j \right) x_n.$$

Now the positive factor x_n affects the speed with which the trajectories are traveled, but not the shape of the trajectories themselves.

In other words, the trajectories in y space are given by

$$\dot{y}_i = y_i \left(a_{in} + \sum_{j=1}^{n-1} a_{ij} y_j \right) \qquad i = 1, \ldots n-1.$$

If we consider a general matrix (and then modify it to get the bottom row zero) we have proved

Theorem

[Hofbauer.] *The differentiable invertible map $x \mapsto y$ given above maps the orbits of the replicator equation with linear fitness $f_i = (Ax)_i$ onto the orbits of the Lotka-Volterra equation*

$$\dot{y}_i = y_i \left(r_i + \sum_{j=1}^{n-1} b_{ij} y_j \right) \qquad i = 1, \ldots n-1$$

where

$$r_i = a_{in} - a_{nn} \quad \text{and} \quad b_{ij} = a_{ij} - a_{nj}.$$

The steps in this passage from replicator equations to LV are reversible.

Back to the replicator equations with linear fitnesses.

The right hand side of the equation $\dot{x}_i = x_i((Ax)_i - x \cdot Ax)$ vanishes if and only if all the $(Ax)_i$ are equal (in which case they all equal $x \cdot Ax$). So the conditions for such a rest point are the equations

$$(Ax)_1 = \cdots = (Ax)_n, \quad x_1 + \cdots x_n = 1, \quad x_i > 0 \ \forall \ i,$$

n equations in n unknowns, which, therefore, will generically have one or no solutions. These equations are related to certain concepts and equations in game theory:

Nash equilibria.

For a given matrix A a point $p \in \overline{S_n}$ is called a **Nash equilibrium** if

$$x \cdot Ap \leq p \cdot Ap \quad \forall x \in \overline{S_n}.$$

If p is a Nash equilibrium, then taking $x = e_i$ (the i-th unit vector) in the above inequality gives

$$(Ap)_i \leq p \cdot Ap.$$

Multiplying by p_i and summing i gives us back $p \cdot Ap$. So we can not have strict inequality for any i for which $p_i > 0$. We must have

$$(Ap)_i = p \cdot Ap \qquad \forall \ i \text{ for which } p_i > 0.$$

Interior Nash equilibria are rest states of the replicator equation.

In particular, if $p \in S_n$ (the interior of the simplex) - so that all the $p_i > 0$) then we have

$$(Ap)_i = p \cdot Ap \qquad \forall\ i,$$

and so the right hand side of the replicator equation vanishes at p. More generally, if we consider the face of $\overline{S_n}$ spanned by those e_i for which $p_i > 0$, we see that p is a rest point of the replicator equation (restricted ot the interior of that face).

We know that for the Lotka-Volterra equations the existence of an interior ω limit point of any orbit implies the existence of an interior rest point, and we know that the replicator orbits have the same structure as the LV orbits. So we have proved:

Theorem

If $p \in \overline{S_n}$ is a Nash equilibrium of A then it is a rest point for the associated replicator equation.

We also have:

Theorem

If $x(t) \to p \in S_n$ as $t \to \infty$ for some orbit then it is a Nash equilibrium.

Proof.

Suppose that p is *not* a Nash equilibrium. Then for some i we have $(Ap)_i - p \cdot Sp > 2\epsilon > 0$. Since $x(t) \to p$, this means that for sufficiently large t we have $\dot{x}_i/x_i > \epsilon$ which is clearly impossible. $\square$

Evolutionary stable states.

A point $p \in S_n$ is called an **evolutionary stable state** if

$$p \cdot Ax > x \cdot Ax \quad \forall\, x \neq p, \quad x \in S_n.$$

Theorem

[Zeeman.] *If p is an evolutionary stable state then every orbit of the associated replicator equation in the open simplex S_n converges to p.*

$\log x \leq x - 1.$

For the proof of the theorem we will use the inequality

$$\log x \leq x - 1$$

for $x > 0$ with strict inequality when $x \neq 1$.
To prove this inequality observe that both sides are equal when $x = 1$. For $x > 1$ the derivative of the right hand side is 1 while the derivative of the left hand side is $1/x < 1$, so the right hand side is increasing faster. For $x < 1$ we have $1/x > 1$ so the left hand side is increasing faster, and so is strictly below $x - 1$. $\square$

$\sum p_i \log x_i \leq \sum p_i \log p_i$ with strict inequality unless $x_i = p_i$ for all i.

To prove this:

$$\sum p_i \log x_i - \sum p_i \log p_i = \sum p_i \log \frac{x_i}{p_i} \leq \sum p_i \left(\frac{x_i}{p_i} - 1 \right)$$

$$= \sum x_i - \sum p_i = 1 - 1 = 0.$$

The inequality becomes strict if any $x_i \neq p_i$. $\square$

So the function $V(x) = \sum p_i \log x_i$ achieves its maximum at p. We shall show that if p is an evolutionary stable state then V is a Liapounov function for the associated replicator equation.

Indeed,

$$\dot{V} = \sum p_i \frac{\dot{x}_i}{x_i} = \sum p_i \left((Ax)_i - x \cdot Ax\right) = p \cdot Ax - x \cdot Ax > 0$$

if $x \neq p$. $\square$

The function $\mathrm{Ent}(x) := -\sum x_i \log x_i$ (known as the entropy) plays a key role in thermodynamics, statistical mechanics, and information theory. As a diversion, I will spend the last few slides of today's lecture trying to explain why and how this enters into communication theory.

Codes.

We use the following notations. W will be a set of "words", $W = \{a, b, c, d, \dots\}$. The number of elements in W will be denoted by N. A **message** is just a concatenation of words, i.e. a string of elements of W.
Σ will denote an alphabet of D symbols (usually $D = 2$ and the symbols are 0 and 1). A **code** or an **encoding** is a map from W to strings on Σ. It then extends by concatenation to messages.

Example.

$$W = \{a, b, c, d\} \quad \phi : \ a \mapsto 0, \ b \mapsto 111, \ c \mapsto 110, \ d \mapsto 101.$$

Then

$$\phi(aba) = 01110.$$

Uniquely decipherable codes and instantaneous codes.

A code, ϕ, is called **uniquely decipherable** (UD) if any string S on Σ has at most one preimage under ϕ. A code is called **instantaneous** (INS) if no $\phi(w)$ occurs as a prefix of the code for some other word. Clearly every instantaneous code can be uniquely deciphered, each word as it arrives. Hence

$$\mathrm{UD} \supset \mathrm{INS}.$$

Example. $W = \{x, y\}, \Sigma = \{0, 1\}, \phi : \; x \mapsto 0, \; y \mapsto 01.$ Then

$$00010101$$

deciphers from the end as $xxyyy$. But we needed to wait until the end of the message to decode. If the last digit had been a 0 instead of a 1, it would have decoded as $xxyyxx$. So the inclusion is strict.

Frequencies.

We let $|S|$ denote the length (number of elements in) a string S. Suppose that the messages sent are all such that each word w occurs with a relative frequency $f(w)$, so we think of f as a probability measure on W. So now $f(w)$ denotes frequency rather than fitness.

Then the expectation

$$E(|\phi(w)|) = E_f(|\phi(w)|) = \sum f(w)|\phi(w)|$$

is the "average length of the encoding ϕ". We would like to make this as small as possible.

We define

$$\mathrm{Ent}(f) = E(-\log f) = -\sum_w f(w) \log f(w)$$

as before.

Shannon's "first theorem".

Theorem

For any UD code, ϕ we have

$$E(|\phi(w)|) \geq \frac{\mathrm{Ent}(f)}{\log D}. \tag{3}$$

There exists an INS code ϕ such that

$$E(|\phi(w)|) \leq \frac{\mathrm{Ent}(f)}{\log D} + 1. \tag{4}$$

McMillan's inequality.

I will prove (3) by first proving *McMillan's inequality*: Let $\ell_1, \ldots, \ell_N$ be the code word lengths of a UD code. Then McMillan's inequality says that

$$\sum_1^N D^{-\ell_i} \leq 1. \tag{5}$$

The proof of McMillan's inequality will be by the method of generating functions:

For any integer r we have

$$\left(D^{-\ell_1}+D^{-\ell_2}+\cdots+D^{-\ell_N}\right)^r=\sum_1^{r\ell} b_i D^{-i}$$

where $\ell = \max \ell_j$ and where b_i denotes the number of ways that a string of length i can be constructed by concatenating r code words. Now there are D^i strings of length i in all. If the code is uniquely decipherable then there can't be more than D^i messages whose code is a string of length i. Hence

$$b_i \le D^i$$

and plugging into the preceding equality gives

$$\left(D^{-\ell_1}+D^{-\ell_2}+\cdots+D^{-\ell_N}\right)^r \le r\ell.$$

We have shown that

$$\left(D^{-\ell_1} + D^{-\ell_2} + \cdots + D^{-\ell_N}\right)^r \leq r\ell.$$

Hence

$$D^{-\ell_1} + D^{-\ell_2} + \cdots + D^{-\ell_N} \leq \ell^{1/r} r^{1/r} \to 1$$

as $r \to \infty$. This proves McMillan's inequality (5).

Now to the proof of Shannon's inequality (3):

Set

$$q_i = \frac{D^{-\ell_i}}{D^{-\ell_1} + D^{-\ell_2} + \cdots + D^{-\ell_N}}$$

so that

$$\sum q_i = \sum f_i = 1$$

where $f_i = f(w_i)$ is the frequency of the $i-$th word. We have proved that

$$\mathrm{Ent}(f) = -\sum f_i \log f_i \leq -\sum f_i \log q_i = \log D \sum f_i \ell_i + \log(\sum_1^N D^{-\ell_i}).$$

But $(\sum_1^N D^{-\ell_i}) \leq 1$ and hence its logarithm is negative. We conclude that

$$\mathrm{Ent}(f) \leq \log D \times E(|\phi(w)|)$$

which is just (3). $\square$

Krafts lemma.

We now show that there exists an instantaneous code satisfying (4). For this we need Kraft's lemma

Lemma

For any ℓ_i satisfying

$$\sum_1^N D^{-\ell_i} \leq 1, \qquad (5)$$

there exists an instantaneous code whose word lengths are ℓ_i.

Proof of Kraft's lemma, I.

Write (5) as

$$\sum_{1}^{\ell} n_j D^{-j} \leq 1$$

where n_i is the number of ℓ_i which are equal to j. Multiply through by D^ℓ and move terms to the other side so the inequality becomes

$$n_\ell \leq D^\ell - n_1 D^{\ell-1} - \cdots - n_{\ell-1} D.$$

Now the n_ℓ which occurs on the left of the inequality is a non-negative (actually positive) integer. So we certainly have the inequality

$$0 \leq D^\ell - n_1 D^{\ell-1} - \cdots - n_{\ell-1} D.$$

Proof of Kraft's lemma, II.

$$0 \leq D^{\ell} - n_1 D^{\ell-1} - \cdots - n_{\ell-1} D.$$

Dividing by D and bringing $n_{\ell-1}$ over to the other side gives

$$n_{\ell-1} \leq D^{\ell-1} - n_1 D^{\ell-2} - \cdots - n_{\ell-2} D.$$

So proceding in this way we get the string of inequalities:

Proof of Kraft's lemma, III.

$$
\begin{aligned}
n_\ell &\leq D^\ell - n_1 D^{\ell-1} - \cdots - n_{\ell-1} D \\
n_{\ell-1} &\leq D^{\ell-1} - n_1 D^{\ell-2} - \cdots - n_{\ell-2} D \\
n_{\ell-2} &\leq D^{\ell-2} - n_1 D^{\ell-3} - \cdots - n_{\ell-3} D \\
&\vdots \\
n_3 &\leq D^3 - n_1 D^2 - n_2 D \\
n_2 &\leq D^2 - n_1 D \\
n_1 &\leq D.
\end{aligned}
$$

Proof of Kraft's lemma, IV.

Let us read these inequalities in reverse order. The last inequality says that we can encode n_1 words each by a single letter from the alphabet Σ, with $D - n_1$ letters left over to serve as prefixes of code words. The next to last inequality says that we can encode n_2 words as two letter code words using the $D - n_1$ letters as first letters and choosing from the D letters as second letters, $D^2 - n_1 D = (D - n_1)D$ possibilities in all. This leave $D^2 - n_1 D - n_2$ possible prefixes for three letter words, and the third from last inequality says that we have enough room to encode n_3 words as three letter code words. Proceeding in this way back up to the top proves Kraft's lemma. $\square$

Proof of the second assertion in Shannon's theorem using Kraft's lemma.

Choose word lengths ℓ_i to be the smallest integers satisfying

$$f_i^{-1} \leq D^{\ell_i}.$$

This is equivalent to

$$\ell_i \log D \geq -\log f_i$$

and

$$\ell_i \leq 1 - \frac{\log f_i}{\log D}$$

since we have chosen ℓ_i as small as possible.

But

$$\sum D^{-\ell_i} \leq \sum f_i = 1$$

so (5) is satisfied, and we can find an instantaneous code with the word lengths ℓ_i. For this code we have

$$\sum f_i \ell_i \leq \sum f_i \left(1 - \frac{\log f_i}{\log D}\right) = 1 + \frac{\operatorname{Ent}(f)}{\log D}. \qquad \square$$

Here are photographs of Lotka and Volterra:

Alfred James **Lotka** (1880 – 1949)

Vito Volterra

1860 - 1940

Here is a photograph of Shannon:

Claude E Shannon

1916 - 2001