Lotka–Volterra Dynamical Systems

Chapter · February 2017

DOI: 10.1142/9781786341044_0005

1 author:

Stephen Baigent
University College London

Chapter 1

Lotka-Volterra Dynamical Systems

Stephen Baigent
Department of Mathematics, UCL, Gower Street, London WC1E 6BT
steve.baigent@ucl.ac.uk

Lotka-Volterra systems are used to introduce in a simple setting a number of dynamical systems techniques. Concepts such as omega limit sets, simple attractors, Lyapunov functions are explained in the context of Lotka-Volterra systems. We discuss LaSalle's Invariance principle. Monotone systems theory is also introduced in the context of the Lotka-Volterra systems.

1. Introduction and scope

The Lotka-Volterra equations are an important model that has been widely used by theoretical ecologists to study the implications of various interactions between members of a population in a fixed habitat containing a number of distinct interacting species. They are by no means the most realistic of such ecological models, but they are arguably the simplest since the highest order terms they involve are quadratic, and therefore they feature the next level of complexity up from linear. As we shall see, even amongst differential equations with quadratic terms, they have a very special form which makes them amenable to well-known mathematical techniques from standard linear algebra, convex analysis, and dynamical systems theory.

To set the scene, we write the Lotka-Volterra equations in the revealing form:

$$\frac{\dot{x}_i}{x_i} = r_i + \sum_{j=1}^{n} a_{ij} x_j, \tag{1}$$

where n is the number of distinct species, x_i is the population density of the ith species, and r_i, a_{ij} are all real numbers, possibly zero, and here assumed to be independent of time. Multiplying each equation through by x_i shows that indeed the equations are quadratic, but when written as above we see that the net population growth per individual per unit time ($\dot{x}_i/x_i$) is linear in the population densities $x = (x_1, \ldots, x_n)$.

A good starting point in the study of the dynamics of (1) is to first locate steady states; that is, points x^* where $\dot{x}_i = 0$ for each $i = 1, \ldots, n$. Of special interest, since they model one scenario where all species can coexist, are the so-called *interior* steady states. These satisfy $x_i^* > 0$ for each $i = 1, \ldots, n$ and so are obtained by solving the linear system

$$r_i + \sum_{j=1}^{n} a_{ij} x_j, \ i = 1, \ldots, n. \tag{2}$$

Recall that the r_i, a_{ij} may be of any sign or zero. As we shall see, determining when (2) has a unique solution $x_i^* > 0$ for each $i = 1, \ldots, n$ relies heavily on linear algebraic techniques. All other steady states involve at least one density vanishing; that is at least one species is extinct. Such steady states are determined by investigating the linear system (2) with all possible subsets of $\{x_i\}_{i=1}^n$ set to zero.

The main virtue of model (1) is that it enables us to study on paper or on the computer the outcome of any set of interactions between the n species, and they are the simplest model that enables us to do so. The type of interactions we refer to are split into two categories: *intraspecific* (the effect of one member of a species on another member of the same species), and *interspecific* (the effect of a member of one species on a member of another species). The strength of the interactions are encoded in the parameters a_{ij}, which are usually assembled into the $n \times n$ interaction matrix $A = ((a_{ij}))$. The parameters r_i determines the *intrinsic* growth rate per individual of species i which would be observed if intraspecific and interspecific interactions were absent. Here we will not be concerned with the precise details of the ecological or environmental mechanisms that contribute to the value of each of the parameters, as we are more interested in the effects of the signs and magnitudes of each parameter on the qualitative behaviour of (1).

We shall however, link the signs of parameters to types of interactions. For example, $r_i > 0$ says that the environment intrinsically favours the growth of species i, whereas $r_i < 0$ signals a risk of extinction for that species unless the presence of another species promotes its growth. An example of the latter case is where a predator will go extinct in the absence of its prey and a suitable substitute food source.

Much of the material will apply to the most general form of the Lotka-

Volterra model (1). Existence of interior steady states will be investigated and their local stability studied.

2. Lyapunov methods for Lotka-Volterra Systems

2.1. *Some basic dynamical systems results*

Sime notation first: $\mathbb{R}_{\geq 0} = \{x \geq 0\}$, $\mathbb{R}_{>0} = \{x > 0\}$. We will always assume that parameters are such that the differential equations (1) generate a semiflow $\varphi_t : \mathbb{R}^n_{\geq 0} \to \mathbb{R}^n_{\geq 0}$: $\forall x \in \mathbb{R}^n_{\geq 0}$ and $s, t \geq 0$,

(1) $\varphi_0(x) = x$;
(2) $\varphi_t(\varphi_s(x)) = \varphi_{t+s}(x)$;

Let $U \subset \mathbb{R}^n$ be open.

Definition 1 (Orbit). The (forward) orbit of $x \in U$ is the set $O^+(x) = \{\varphi_t(x) : t \geq 0\}$.

Definition 2 (Steady state). A steady state of $\dot{x} = f(x)$ is a point $x \in U$ for which $f(x) = 0$.

Definition 3 (Forward invariant set). A set $S \subseteq U$ is a forward invariant set for φ_t if whenever $x \in S$ we have $\varphi_t(x) \in S$ for all $t \geq 0$.

Definition 4 (Invariant set). When φ_t is a flow (i.e. also defined for $t \leq 0$), the set $S \subseteq U$ is an invariant set for φ_t if whenever $x \in S$ we have $\varphi_t(x) \in S$ for all $t \in \mathbb{R}$.

One important use of invariant sets is captured by the following result:[2]

Theorem 1. *Let $S \subset \mathbb{R}^n$ be homeomorphic to the closed unit ball and forward invariant for the flow of $\dot{x} = f(x)$. Then the flow has a steady state $x^* \in S$.*

Hence one way of showing the existence of at least one steady state in a compact simply-connected subset of $\mathbb{R}^n$ is to show that all orbits enter that set (so that it is forward invariant).

The Heine-Borel theorem states that a subset of $\mathbb{R}^n$ is compact if and only if it is closed and bounded. The key tool for studying the convergence of orbits is the *Omega limit set.* This is the totality of all limit points of the forward orbit through a given point. To prove that an orbit is convergent to a steady state, one needs to show that its omega limit set consists of a single point, namely that steady state. Other interesting limit sets are attracting limit cycles, periodic orbits, attractors, etc.

Definition 5 (Omega limit point). A point $p \in U$ is an omega limit point of $x \in U$ if there are points $\varphi_{t_1}(x), \varphi_{t_2}(x), \ldots$ on the orbit of x such that $t_k \to \infty$ and $\varphi_{t_k}(x) \to p$ as $k \to \infty$.

Definition 6 (Omega limit set). The omega limit set $\omega(x)$ of a point $x \in U$ under the flow φ_t is the set of all omega limit points of x.

There is a similar construct for when φ_t is defined backwards in time, such as when it is a flow:

Definition 7 (Alpha limit point). A point p is an α limit point for the point $x \in U$ if there are points $\varphi_{t_1}(x), \varphi_{t_2}(x), \ldots$ on the orbit of x such that $t_k \to -\infty$ and $\varphi_{t_k}(x) \to p$ as $k \to \infty$.

Definition 8 (Alpha limit set). The alpha limit set $\alpha(x)$ of a point $x \in U$ under the flow φ_t is the set of all alpha limit points of x.

Lemma 1 (Properties of Omega limit sets).

(1) $\omega(x)$ *is a closed set (but it might be empty);*
(2) If $\overline{O^+(x)}$ *is compact, then* $\omega(x)$ *is non-empty and connected;*
(3) $\omega(x)$ *is an invariant set for* φ_t*;*
(4) If $y \in O^+(x)$ *then* $\omega(y) = \omega(x)$*;*
(5) $\omega(x)$ *can be written as*

$$\omega(x) = \bigcap_{t \geq 0} \overline{\{\varphi_s(x) : s \geq t\}} = \bigcap_{t \geq 0} \overline{O^+(\varphi_t(x))},$$

where $\overline{A}$ *is the closure of* A*.*

For a proof see, for example, reference 4.

Example 1. $\dot{x} = 1$ has the flow $\varphi_t(x) = x + t$. Given any $x \in \mathbb{R}$ and any sequence $t_k \to \infty$, $\varphi_{t_k}(x) \to \infty$ and hence $\omega(x)$ is empty. On the other hand, for $\dot{x} = ax$ the flow is $\varphi_t(x) = e^{at}x$, so that $\varphi_{t_k}(x) = e^{at_k}x \to 0$ as $t_k \to \infty$ if $a < 0$ giving $\omega(x) = \{0\}$ and clearly $\varphi_t(0) = 0$ so $\omega(x)$ is indeed invariant. But if $a > 0$ the set $\omega(x)$ is empty.

As another example, take

Example 2.

$$\begin{aligned}\dot{x} &= x - y - x(x^2 + y^2)\\ \dot{y} &= x + y - y(x^2 + y^2).\end{aligned} \tag{3}$$

By multiplying the first equation by x and the second by y and adding we obtain, after setting $r = \sqrt{x^2 + y^2}$ and simplifying, $\dot{r} = r - r^3$. The set $r = 1$ i.e. $\mathbb{S} = \{(x, y) : x^2 + y^2 = 1\}$ is an invariant set and $(x, y) = (0, 0)$ is the unique steady state. It is not difficult to see that any orbit is either the unique steady state $(0, 0)$, the unit circle, or a spiral that tends towards the unit circle. If $(x, y) \neq (0, 0)$, $\omega((x, y)) = \mathbb{S}$, and otherwise $\omega((0, 0)) = \{(0, 0)\}$.

Problem 1. *Find the omega limit sets for the predator-prey system on* $\mathbb{R}^2_{\geq 0}$

$$\begin{aligned}\dot{x} &= x(1 - x + y)\\ \dot{y} &= y(-1 - y + x).\end{aligned}$$

The many practical uses of the omega limit set is typified by the following result. Note that $\dot{x} = 1/x$ with $x(0) > 0$ satisfies $\dot{x} \to 0$ as $t \to \infty$, but the unique forward orbit $x(t) = \sqrt{2t + x(0)^2} \to \infty$ as $t \to \infty$ does not converge to a steady state. However, we do have:

Lemma 2. *Suppose that* $f : \mathbb{R}^n \to \mathbb{R}^n$ *is continuously differentiable with isolated zeros. If* $x : \mathbb{R}_{\geq 0} \to \mathbb{R}^n$ *is a bounded forward orbit of* $\dot{x} = f(x)$ *such that* $\dot{x}(t) \to 0$ *as* $t \to \infty$*, then* $x(t) \to p$ *for some* p *as* $t \to \infty$ *where* $f(p) = 0$*, i.e.* x *converges to a steady state.*

Proof. Let the orbit pass through x_0. $\overline{O^+(x_0)}$ is bounded and hence compact, so $\omega(x_0)$ is compact, connected and nonempty. For $p \in \omega(x_0)$ there exists a sequence $t_k \to \infty$ as $k \to \infty$ such that $x(t_k) \to p$ as $k \to \infty$. By continuity $0 = \lim_{k\to\infty} \dot{x}(t_k) = \lim_{k\to\infty} f(x(t_k)) = f(p)$, so that p is a steady state. Thus $\omega(x_0)$ consists entirely of steady states. Since $\omega(x_0)$ is connected, and the steady states are isolated, $\omega(x_0) = \{p\}$. $\square$

2.2. *Stability*

Definition 9 (Lyapunov stability). A steady state x^* is said to be Lyapunov stable if for any $\epsilon > 0$ (arbitrarily small) $\exists\ \delta > 0$ such that $\forall x_0$ with $|x^* - x_0| < \delta$ we have $|\varphi(x_0, t) - x^*| < \epsilon$ for all $t \geq 0$.

A steady state is said to be unstable if it is not (Lyapunov) stable.

Definition 10 (Asymptotic stability). A steady state x^* is said to be asymptotically stable if it is Lyapunov stable and $\exists\ \rho > 0$ such that $\forall x_0$ with $|x^* - x_0| < \rho$ we have $|\varphi(x_0, t) - x^*| \to 0$ as $t \to \infty$.

For example, in the system $\dot{x} = -x - y + x(x^2 + y^2), \dot{y} = x - y + y(x^2 + y^2)$, the origin is locally asymptotically stable (we get $\dot{r} = -r + r^3$ by using polar coordinates). For a simple harmonic oscillator in the form of a pendulum, the pendulum resting vertically downwards is Lyapunov stable but not asymptotically stable unless there is damping such as air resistance. The upward vertical state of the pendulum is an example of an unstable steady state.

Definition 11 (Basin of attraction). The basin of attraction $B(x^*)$ of a steady state $x^* \in U$ is the set of points $y \in U$ such that $\varphi_t(y) \to x^*$ as $t \to \infty$.

Definition 12 (Global stability). If $B(x^*) = U$ then x^* is said to be globally asymptotically stable on U.

Problem 2. *Consider the logistic equation $\dot{x} = x(1 - x)$. Find all forward invariant and invariant subsets of $\mathbb{R}_{\geq 0}$ and obtain the basin of attraction of the positive steady state.*

3. Ecological Systems

Consider the model

$$\dot{x}_i = x_i f_i(x), \quad i = 1, \ldots, n. \tag{4}$$

where each $f_i : \mathbb{R}^n \to \mathbb{R}^n$ is C^1. Suppose that $x(0) = (x_{01}, \ldots, x_{0n})$ has $x_{0k} = 0$ for $k \in J \subset \{1, \ldots, n\}$, so that some species are initially absent. Then these species are absent for all time for which the solutions exist:

Theorem 2. *For the model (4) the coordinate axes and the subspaces spanned by them, and $\mathbb{R}^n_{>0}$, are all forward invariant.*

In other words populations that start nonnegative remain nonnegative. Populations starting positive cannot go to zero in finite time.

4. LaSalle's Invariance Principle

We start with a basic result for Lyapunov functions (e.g. page 127 in reference 13):

Theorem 3. *Let $U \subseteq \mathbb{R}^n$ be open and $f : U \to \mathbb{R}$ be continuously differentiable and such that $f(x_0) = 0$ for some $x_0 \in U$. Suppose further that there is a real-valued function $V : U \to \mathbb{R}$ that satisfies (i) $V(x_0) = 0$, (ii) $V(x) > 0$ for $x \in U \setminus \{x_0\}$. Then if (a) $\dot{V}(x) := \nabla V(x) \cdot f(x) \leq 0$ for all $x \in U$ then x_0 is Lyapunov stable; if $\dot{V}(x) < 0$ for all $U \setminus \{x_0\}$ then x_0 is asymptotically stable on U; (c) if $\dot{V}(x) > 0$ for all $x \in U \setminus \{x_0\}$, x_0 is unstable.*

This is a powerful theorem, but there is a useful generalisation of it which caters for when $\dot{V}^{-1}(0)$ is not an isolated point.

Theorem 4 (LaSalle's Invariance Principle). *Let $\dot{x} = f(x)$ define a flow on a set $U \subseteq \mathbb{R}^n$, where f is continuously differentiable. Suppose $V : U \to \mathbb{R}$ is a continuously differentiable function. Let Q be the largest invariant subset of U. If for some bounded solution $x(t, x_0)$ with initial condition $x(0, x_0) = x_0 \in U$ the time derivative $\dot{V} = DVf$ satisfies $\dot{V}(x(t, x_0)) \leq 0$, then $\omega(x_0) \subseteq Q \cap \dot{V}^{-1}(0)$.*

Proof. By boundedness of the orbit, $\omega(x)$ is nonempty and for $p \in \omega(x)$ there exists a $t_k \to \infty$ such that $x(t_k) \to p$. Since $\dot{V}(x(t_k)) \leq 0$ the sequence $\{V(t_k)\}$ is nonincreasing. Since $x(t_k, x_0)$ is bounded, $V(x(t_k, x_0))$ is bounded, so that there exists a $c \in \mathbb{R}$ such that $V(t_k) \to c$. Hence $\omega(x) \subset V^{-1}(c)$. Since $\omega(x_0)$ is invariant, $\omega(x_0) \subset Q$, and for any $y \in \omega(x_0)$ we have $V(x(t, y)) = c$ and differentiating gives $\dot{V}(x(t, y)) = 0$ for all t, and hence $\dot{V}(y) = 0$ for all $y \in \omega(x)$. Hence $\omega(x) \subset Q \cap \dot{V}^{-1}(0)$. $\square$

Example 3.

$$
\begin{aligned}
\dot{x} &= x - y - x(x^2 + y^2) \\
\dot{y} &= x + y - y(x^2 + y^2).
\end{aligned}
$$

Taking $U = \mathbb{R}^2$, $V(x, y) = \sqrt{x^2 + y^2}$ we get

$$
\frac{dV}{dt} = V(1 - V^2) \begin{cases} \leq 0 & \text{for } |(x, y)| \geq 1 \\ > 0 & |(x, y)| < 1. \end{cases}
$$

Thus $\dot{V}^{-1}(0) = \{(0, 0)\} \cup \mathbb{S}$ ($\mathbb{S}$ is the unit circle). $Q = \mathbb{R}^2$ and applying LaSalle's invariance principle we get $\omega((x, y)) \subset \{(0, 0)\} \cup \mathbb{S}$. But the omega limit set is also connected, so that it must be either $\{(0, 0)\}$ or (by invariance) all of $\mathbb{S}$. Since $(0, 0)$ is unstable, we must have $\omega(x_0) = \mathbb{S}$ when $x_0 \neq 0$ and $\omega((0, 0)) = \{(0, 0)\}$.

Example 4.

$$\dot{x} = x(-\alpha + \gamma y) \tag{5}$$

$$\dot{y} = \alpha x - (\gamma x + \delta)y \quad (\alpha, \beta, \delta > 0) \tag{6}$$

This system has a unique steady state $(0, 0)$, and one can show that $U = \mathbb{R}^2_{\geq 0}$ is forward invariant. Adding (5) and (6) we obtain

$$\frac{d}{dt}(x + y) = -\delta y \leq 0 \text{ on } \mathbb{R}^2_{\geq 0}.$$

Take $V(x, y) = x + y$. Then $\dot{V}^{-1}(0) = \{(s, 0) : s \in \mathbb{R}\}$. By LaSalle's invariance principle,

$$\omega((x, y)) \subseteq \{(s, 0) : s \in \mathbb{R}_{\geq 0}\}, \ \ (x, y) \in \mathbb{R}^2_{\geq 0}.$$

But $\omega((x, y))$ must be connected and invariant, and the only invariant subsets of $T = \{(s, 0) : s \in \mathbb{R}_{>0}\}$ for the flow of (5) and (6) are the origin and T itself. But, by (5), for $s \geq 0$, $\varphi_{t_k}(s, 0) \to (0, 0)$ for any sequence $t_k \to \infty$, so $\omega((x, y)) = \{(0, 0)\}\ \forall (x, y) \in \mathbb{R}^2_{\geq 0}$.

Theorem 5 (Goh[7]). *Suppose that the Lotka-Volterra system* $\dot{x}_i = x_i f_i(x) = x_i(r_i + \sum_{j=1}^n a_{ij} x_j)$, $i = 1, \ldots, n$ *has a unique interior steady state* $x^* = -A^{-1}r \in \mathbb{R}^n_{>0}$*. Then this steady state is globally attracting on* $\mathbb{R}^n_{>0}$ *if there exists a diagonal matrix* $D > 0$ *such that* $AD + DA^T$ *is negative definite.*

Proof. Let $V : \mathbb{R}^n_{\geq 0} \to \mathbb{R}_{\geq 0}$ be defined by

$$V(x) = \sum_{i=1}^n \alpha_i \left(x_i - x_i^* - x_i^* \log(x_i/x_i^*)\right),$$

where $\alpha_i \in \mathbb{R}_{>0}$ are to be found. Then we compute

$$\dot{V} = \nabla V \cdot f = \sum_{i=1}^n \alpha_i (x_i - x_i^*) f_i(x) = \sum_{i=1}^n \alpha_i (x_i - x_i^*) \left\{ \sum_{j=1}^n a_{ij}(x_j - x_j^*) \right\}.$$

This can be rewritten as

$$\dot{V} = (x - x^*)^T A^T D (x - x^*) = \frac{1}{2}(x - x^*)^T (DA + A^T D)(x - x^*),$$

where $D = \mathrm{diag}(\alpha_1, \ldots, \alpha_n)$. When $DA + A^T D$ is negative definite, $\dot{V} \leq 0$ and $\dot{V}^{-1}(0) = \{x^*\}$. V is convex (as the sum of convex functions) and has a unique minimum at $x = x^*$. Hence by Theorem 3 x^* is globally asymptotically stable on $\mathbb{R}^n_{>0}$. $\square$

(See reference 16 for an improvement of this result to cater for boundary steady states.)

Example 5. Consider the two species Lotka-Volterra system

$$\begin{aligned}\dot{x} &= x(a + bx + cy)\\ \dot{y} &= y(d + ex + fy).\end{aligned} \tag{7}$$

Suppose that (7) has a unique interior steady state, say $(x^*, y^*) \in \mathbb{R}^2_{>0}$. Thus $bf - ce \neq 0$. We use Theorem 5. Let $\lambda > 0$ and

$$D = \begin{pmatrix} 1 & 0 \\ 0 & \lambda \end{pmatrix}, \; M = DA + A^T D = \begin{pmatrix} 2b & c + \lambda e \\ c + \lambda e & 2\lambda f \end{pmatrix}.$$

Then for diagonal stability we need M to negative definite, which it is if and only if its trace is negative and its determinant is positive:

$$\text{(i) } \lambda f + b < 0, \;\; \text{(ii) } 4bf\lambda > (c + \lambda e)^2.$$

Since we seek $\lambda > 0$, to satisfy (ii) we require $fb > 0$, which then implies $f, b < 0$ by (i). Next for (ii) we need

$$4bf\lambda - (c + \lambda e)^2 = (4bf - 2ce)\lambda - c^2 - e^2\lambda^2 > 0$$

for some $\lambda > 0$. The quadratic $\phi(\lambda) = (4bf - 2ce)\lambda - c^2 - e^2\lambda^2$ is negative for $\lambda = 0$ and large $|\lambda|$, and so is positive for some $\lambda > 0$ only if $4bf - 2ec = 2\det A + 2bf > 0$ and $(4bf - 2ce)^2 > 4e^2c^2$ which simplifies to $\det A > 0$.

To conclude, we have shown

Theorem 6 (Goh[6]). *Suppose the system*

$$\begin{aligned}\dot{x} &= x(a + bx + cy)\\ \dot{y} &= y(d + ex + fy).\end{aligned} \tag{8}$$

has a unique interior steady state $(x^*, y^*) \in \mathbb{R}^2_{>0}$. *Then* (x^*, y^*) *globally attracts all points in* $\mathbb{R}^2_{>0}$ *if* $f < 0, b < 0$ *and* $\det A > 0$.

Problem 3. *Is the converse of Theorem 6 true?*

5. Conservative Lotka-Volterra Systems

Definition 13 (Conservative Lotka-Volterra). We will say that (1) is conservative if there exists a diagonal matrix $D > 0$ such that AD is skew-symmetric.

Notice that if B is skew-symmetric then $b_{ij} = -b_{ji}$ for all i, j. In particular $b_{ii} = -b_{ii}$ so that $b_{ii} = 0$, i.e. the diagonal elements of a skew-symmetric matrix are all zero.

Problem 4. *Consider the two-species Lotka-Volterra system*

$$\frac{1}{N}\frac{dN}{dt} = a - bP$$
$$\frac{1}{P}\frac{dP}{dt} = cN - d$$

Change to new coordinates $x = \log N, y = \log P$ *and show that* $H(x, y) = dx + ay - e^x - e^y$ *is constant along a trajectory* $(x(t), y(t))$. *Show also that* $\dot{x} = \frac{\partial H}{\partial y}, \dot{y} = -\frac{\partial H}{\partial x}$.

A change of coordinates $y_i = x_i/d_i$ $(d_i \leq 0)$ transforms (1) into

$$\dot{y}_i = y_i(r_i + \sum_{j=1}^{n} d_j a_{ij} y_j),$$

so that we obtain another Lotka-Volterra system with interaction matrix AD. The Lotka-Volterra systems with interaction matrices AD for $D > 0$ diagonal have topologically equivalent dynamics.

Lemma 3. *If* A *is an* $n \times n$ *skew-symmetric matrix then* $\det A = (-1)^n \det A$. *Hence when* n *is odd,* A *is singular.*

Proof. $\det A = \det A^T = \det(-A) = (-1)^n \det A$. $\square$

Now suppose that A is skew-symmetric. We will show that certain Lotka-Volterra systems can be written in Hamiltonian form. But before doing so, we recall the definition of a Hamiltonian system on $\mathbb{R}^n$ (see, for example, reference 12). Let C^∞ denote the space of smooth functions $\mathbb{R}^n \to \mathbb{R}$.

Definition 14 (Hamiltonian system on $\mathbb{R}^n$). A Hamiltonian system (on $\mathbb{R}^n$) is a pair $(H, \{\cdot,\cdot\})$ where $H : \mathbb{R}^n \to \mathbb{R}$ is a smooth function, called the Hamiltonian, and $\{\cdot,\cdot\} : C^\infty \times C^\infty \to C^\infty$ is a Poisson bracket; that is a bilinear skew-symmetric map $\{\cdot,\cdot\} : C^\infty \times C^\infty \to C^\infty$ that satisfies the following relations for all $f, g, h \in C^\infty$

(1) $\{f, gh\} = \{f, g\}h + g\{f, h\}$ [Leibnitz rule] ;
(2) $\{f, \{g, h\}\} + \{g, \{h, f\}\} + \{h, \{f, g\}\} = 0$ [Jacobi Identity] .

For example, when $n = 2$ the bracket $\{\cdot,\cdot\} : C^\infty \times C^\infty \to \mathbb{R}$ given by

$$\{f, g\} = \frac{\partial f}{\partial q}\frac{\partial g}{\partial p} - \frac{\partial f}{\partial p}\frac{\partial g}{\partial q}$$

defines a Poisson bracket.

For each $g \in C^\infty$, the bracket defines a Hamiltonian vector field X_g on $\mathbb{R}^n$ via $\{f, g\} = X_g(f)$. In the previous example $X_g = \frac{\partial g}{\partial q}\frac{\partial}{\partial p} - \frac{\partial g}{\partial p}\frac{\partial}{\partial q}$. Hamilton's equations are then given by $\dot{x}_i = X_H(x_i)$ for $i = 1, \ldots, n$. In particular, $\dot{H} = \{H, H\} = 0$ gives the constancy of the Hamiltonian function along an orbit. In addition to conserved functions conserved on orbits, there may also be functions C such that $\{C, f\} = 0$ for all functions $f \in C^\infty$. That is: C is constant along all flows generated by the Hamiltonian vector fields X_f as f ranges through C^∞. Such functions C are known as *Casimirs*.

To establish that a Lotka-Volterra system is Hamiltonian, we thus have to identify both a Poisson bracket and a Hamiltonian function.

Before turning to a Hamiltonian description of (1) we note that there's a graphical way to test whether a Lotka-Volterra system is conservative:

Proposition 1 (Volterra[18]). *The Lotka-Volterra system $\dot{x}_i = x_i(r_i + (Ax)_i)$ is conservative if and only if $a_{ii} = 0$ and $a_{ij} \neq 0 \Rightarrow a_{ij}a_{ji} < 0$, and for every sequence $i_1, i_2, \ldots, i_s$ we have $a_{i_1 i_2}a_{i_2 i_3}\cdots a_{i_s i_1} = (-1)^s a_{i_s i_{s-1}}\cdots a_{i_2 i_1}a_{i_1 i_s}$.*

That is we have a graphical condition that there exists a diagonal matrix $D > 0$ such that AD is skew-symmetric ($AD + DA^T = 0$; compare with Theorem 5). One creates a signed digraph with nodes labelled 1 to n where n is the number of species and puts on each directed edge linking nodes i to j the number a_{ij}. The condition to check is then that for each cycle in the digraph of length s, the product of the edge numbers in one direction is $(-1)^s$ times the product in the opposite direction.

6. Volterra's construction[5,18]

We start with the skew-symmetric system

$$\dot{x}_i = x_i(r_i + \sum_{j=1}^{n} a_{ij}x_j), \quad a_{ij} = -a_{ji}. \tag{9}$$

Volterra introduced new coordinates which he called *quantity of life*:

$$Q_i = \int_0^t x_i(s)\, ds \quad (i = 1, \ldots, n).$$

Thus $\dot{Q}_i = x_i$ and (9) becomes the second order system

$$\ddot{Q}_i = \dot{Q}_i(r_i + \sum_{j=1}^{n} a_{ij}\dot{Q}_j). \tag{10}$$

Then he introduces $H(Q,\dot{Q}) = \sum_{i=1}^{n}(r_iQ_i - \dot{Q}_i)$ so that

$$\frac{dH}{dt} = \sum_{i=1}^{n}(r_i\dot{Q}_i - \ddot{Q}_i) = \sum_{i=1}^{n}(r_i\dot{Q}_i - \dot{Q}_i(r_i + \sum_{j=1}^{n} a_{ij}\dot{Q}_j)) = -\sum_{i,j=1}^{n} a_{ij}\dot{Q}_i\dot{Q}_j = 0$$

using skew-symmetry of $A = ((a_{ij}))$. Dual variables P_i are then defined via

$$P_i = \log\dot{Q}_i - \frac{1}{2}\sum_{j=1}^{n} a_{ij}Q_j \quad (i = 1,\ldots,n).$$

In terms of these new coordinates, we get the transformed $h(Q,P) = H(Q,\dot{Q})$ where

$$h(Q,P) = \sum_{i=1}^{n}\left(r_iQ_i - \exp(P_i + \frac{1}{2}\sum_{j=1}^{n} a_{ij}Q_j)\right).$$

Now we can check that

$$\frac{dQ_i}{dt} = \exp(P_i + \frac{1}{2}\sum_{j=1}^{n} a_{ij}Q_j) = -\frac{\partial h}{\partial P_i},$$

and

$$\begin{aligned}\frac{dP_i}{dt} &= \frac{d}{dt}\left\{\log\dot{Q}_i - \frac{1}{2}\sum_{j=1}^{n} a_{ij}Q_j\right\} \\ &= \frac{\ddot{Q}_i}{\dot{Q}_i} - \frac{1}{2}\sum_{j=1}^{n} a_{ij}\dot{Q}_j = r_i + \sum_{j=1}^{n} a_{ij}\dot{Q}_j - \frac{1}{2}\sum_{j=1}^{n} a_{ij}\dot{Q}_j \\ &= r_i + \frac{1}{2}\sum_{j=1}^{n} a_{ij}\exp(P_j + \frac{1}{2}\sum_{k=1}^{n} a_{jk}Q_k).\end{aligned}$$

On the other hand

$$\frac{\partial h}{\partial Q_i} = r_i - \sum_{k=1}^{n}\frac{a_{ki}}{2}\exp\left(P_k + \frac{1}{2}\sum_{j=1}^{n} a_{kj}Q_j\right) = r_i + \sum_{k=1}^{n}\frac{a_{ik}}{2}\exp\left(P_k + \frac{1}{2}\sum_{j=1}^{n} a_{kj}Q_j\right),$$

using $a_{ik} = -a_{ki}$. This gives $\dot{P}_i = \frac{\partial h}{\partial Q_i}$ as required.

Hence we have shown that the system (9) is canonically Hamiltonian in the new coordinates P, Q with Hamiltonian function

$$h(P,Q) = \sum_{i=1}^{n} \left(r_i Q_i - \exp(P_i + \frac{1}{2}\sum_{j=1}^{n} a_{ij} Q_j) \right),$$

and the standard Poisson bracket

$$\{f, g\} = \sum_{i=1}^{n} \frac{\partial f}{\partial P_i}\frac{\partial g}{\partial Q_i} - \frac{\partial g}{\partial Q_i}\frac{\partial f}{\partial P_i}.$$

7. An alternative Hamiltonian formulation

In the previous formulation, we doubled the number of variables in order to find a Hamiltonian structure. Here we keep the same number of variables as the original Lotka-Volterra system.

Suppose that $Ax + r = 0$ has a solution $x^* \in \mathbb{R}^n$ (here A is skew-symmetric). Introduce new variables $y_i = \log x_i$:

$$\dot{y}_i = (r_i + \sum_{j=1}^{n} a_{ij} \exp y_j) = \sum_{j=1}^{n} a_{ij}(\exp y_j - x_j^*).$$

Now define

$$H(y) = \sum_{i=1}^{n} (\exp y_i - x_i^* y_i),$$

so that

$$\dot{y}_i = \sum_{j=1}^{n} a_{ij}(e^{y_j} - x_j^*) = \sum_{j=1}^{n} a_{ij}\frac{\partial H}{\partial y_j}, \tag{11}$$

$$\begin{aligned} \frac{dH}{dt} &= \sum_{j=1}^{n} \frac{\partial H}{\partial y_j}\dot{y}_j \\ &= \sum_{i=1}^{n}\sum_{j=1}^{n} a_{ij}\frac{\partial H}{\partial y_i}\frac{\partial H}{\partial y_j} \\ &= \frac{1}{2}\sum_{i=1}^{n}\sum_{j=1}^{n}(a_{ij} + a_{ji})\frac{\partial H}{\partial y_i}\frac{\partial H}{\partial y_j} \\ &= 0, \end{aligned}$$

using skew-symmetry of $A = ((a_{ij}))$. To complete the Hamiltonian formulation we check that

$$\{f, g\} = \nabla f \cdot A \nabla g \tag{12}$$

provides a suitable Poisson bracket.

Problem 5. *Show that (12) defines a Poisson bracket.*

Notice that the x^* need not lie in the first quadrant. In an odd dimensional Lotka-Volterra system with skew-symmetric interaction matrix A, we have $\det A = 0$ and it is possible that $Ax + r = 0$ has no solutions. Indeed, if A is singular, then there is a $v \neq 0$ in $\ker A$ such that $v^T A = (A^T v)^T = -(Av)^T = 0$. Thus for a solution to exist we must have $v^T r = 0$ for all $v \in \ker A$, i.e. $r \in (\ker A)^\perp$.

Example 6. Consider the Lotka-Volterra system for 3 interacting species:

$$\begin{aligned} \dot{x}_1 &= x_1(r_1 + \omega_1 x_2 - \omega_2 x_3) \\ \dot{x}_2 &= x_2(r_2 - \omega_1 x_1 + \omega_3 x_3) \\ \dot{x}_3 &= x_3(r_3 + \omega_2 x_1 - \omega_3 x_2) \end{aligned} \tag{13}$$

where $\omega_1, \omega_2, \omega_3 > 0$ and each $r_i > 0$. Here species 3 is prey to species 2. Species 2 consumes species 3, but is consumed by species 1. Species 1 consumes species 2 but it is consumed by species 3. (So we have a cycle of interactions.) It is easy to see that the interaction matrix

$$A = \begin{pmatrix} 0 & \omega_1 & -\omega_2 \\ -\omega_1 & 0 & \omega_3 \\ \omega_2 & -\omega_3 & 0 \end{pmatrix}$$

is skew-symmetric. Since A is 3×3 we already know that A is singular. Thus if q is a solution to $Aq + r = 0$ then so too is $q + k$ for any $k \in \ker A = \{\alpha(\omega_3, \omega_2, \omega_1) : \alpha \in \mathbb{R}\}$. One finds that $Aq + r = 0$ has no solutions (in $\mathbb{R}^3$) unless

$$v^T r = \omega_3 r_1 + \omega_1 r_3 + \omega_2 r_2 = 0 \tag{14}$$

($v = (\omega_3, \omega_2, \omega_1)$) and in this case $q = (\frac{r_2}{\omega_1}, -\frac{r_1}{\omega_1}, 0) + \alpha v$ for $\alpha \in \mathbb{R}$.

Thus let us now assume that (14) holds. For the Hamiltonian we may take

$$H(x) = x_1 + x_2 + x_3 - \frac{r_2}{\omega_1} \log x_1 + \frac{r_1}{\omega_1} \log x_2.$$

We find that

$$\dot{H} = \left(r_3 + \frac{r_2 \omega_2}{\omega_1} + \frac{r_1 \omega_3}{\omega_1} \right) x_3 = 0$$

by virtue of (14). A suitable Poisson bracket is thus

$$\begin{aligned} \{f, g\} &= \omega_1 x_1 x_2 \left(\frac{\partial f}{\partial x_1} \frac{\partial g}{\partial x_2} - \frac{\partial g}{\partial x_1} \frac{\partial f}{\partial x_2} \right) \\ &-\omega_2 x_1 x_3 \left(\frac{\partial f}{\partial x_1} \frac{\partial g}{\partial x_3} - \frac{\partial g}{\partial x_1} \frac{\partial f}{\partial x_3} \right) + \omega_3 x_2 x_3 \left(\frac{\partial f}{\partial x_2} \frac{\partial g}{\partial x_3} - \frac{\partial g}{\partial x_2} \frac{\partial f}{\partial x_3} \right). \end{aligned}$$

Since A is singular, there are Casimir functions C; that is C satisfying $\{C, g\} = 0$ for all g, proportional to

$$C(x) = \omega_3 \log x_1 + \omega_2 \log x_2 + \omega_1 \log x_3.$$

(or we could take $C(x) = x_1^{\omega_3} x_2^{\omega_2} x_3^{\omega_1}$). We find that

$$\dot{C} = r_3\omega_1 + r_2\omega_2 + r_1\omega_3 = 0,$$

again using (14). The dynamics lies on the intersection of the surfaces $H(x) = H(x(0))$ and $C(x) = C(x(0))$ in the first quadrant.

Let us change coordinates, setting $X = \log x_1$, $Y = \log x_2$ and $Z = \log x_3$. Then we have on a solution

$$\begin{aligned} e^X + e^Y + e^Z - \frac{r_2}{\omega_1} X + \frac{r_1}{\omega_1} Y &= A \\ \omega_3 X + \omega_2 Y + \omega_1 Z &= B, \end{aligned}$$

where A, B are constants. Hence we may plot

$$Z = \log\left(A - e^X - e^Y + \frac{r_2}{\omega_1} X - \frac{r_1}{\omega_1} Y \right) \tag{15}$$

$$Z = \frac{B - \omega_3 X - \omega_2 Y}{\omega_1}. \tag{16}$$

The first surface is concave where the logarithm is defined. Searching for periodic orbits then becomes the study of how the surface (15) intersects the plane (16). An example a periodic orbit is shown in Figure 1.

8. Cooperative Lotka-Volterra Systems

We will consider the general Lotka-Volterra system

$$\dot{x}_i = F_i(x) := x_i(r_i + \sum_{j=1}^{n} a_{ij} x_j), \quad (i = 1, \ldots, n). \tag{17}$$

except that we will constrain ourselves to the case that $a_{ij} \geq 0$ when $i \neq j$, i.e. the off-diagonal elements of the interaction matrix are nonnegative. Notice that in this case

$$\frac{\partial F_i}{\partial x_j} = a_{ij} x_i \geq 0, \; i \neq j,$$

since for $i \neq j$ we have $a_{ij} \geq 0$ and we have $x \in \mathbb{R}^n_{\geq 0}$. Since the first quadrant is invariant the Jacobian has nonnegative off-diagonal elements.

Definition 15 (Cooperative matrix). We will say that any real $n \times n$ matrix with nonnegative off-diagonal elements is *cooperative*.

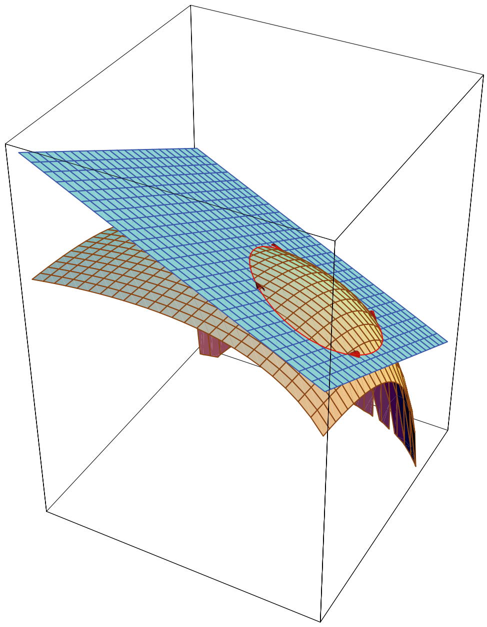

Fig. 1. A periodic solution to the three species model (13). There exists a continuum of periodic orbits around the interior steady state.

Some notation

In what follows we will use the following notation for ordering vectors $x \in \mathbb{R}^n$: For each $x, y \in \mathbb{R}^n$

- $x \leq y \Leftrightarrow x_i \leq y_i$ for all $i = 1, \ldots, n$;
- $x < y \Leftrightarrow x_i \leq y_i$ for all $i = 1, \ldots, n$, but $x_k \neq y_k$ for some k.
- $x \ll y \Leftrightarrow x_i < y_i$ for all $i = 1, \ldots, n$.

(Similarly for $\geq, >, \gg$.) We say that $(\mathbb{R}^n, \leq)$ is an ordered vector space.

The following Perron-Frobenius theorem is fundamental in the study of coorperative or competitive systems (see, for example, reference 3). We recall that the spectral radius of A, written $\rho(A)$, is the modulus of an eigenvalue of A of largest modulus, and a matrix A is irreducible if it is not similar via a permutation to a block upper triangular matrix (that has more than one block of positive size).

Theorem 7 (Perron-Frobenius). *If A is a $n \times n$ real matrix with non-negative entries. Then*

- *$\rho(A)$ is an eigenvalue of A.*
- *A has left and right eigenvectors $u > 0$ and $v > 0$ associated with $\rho(A)$ (i.e. $uA = \rho(A)u$ and $Av = \rho(A)v$).*

If A is also irreducible then we have $\rho(A) > |\mu|$ for any eigenvalue $\mu \neq \rho(A)$, and $\rho(A)$ is simple and $v \gg 0$ and $u \gg 0$ in the above statements.

(Note: the inequalities in Theorem 7 use the vector ordering defined above).

Definition 16. A matrix A is negatively (row) diagonally dominant if there exists a $d \gg 0$ such that $a_{ii}d_i + \sum_{j\neq i} |a_{ij}|d_j < 0$ for all $i = 1, \ldots, n$.

When A is a cooperative matrix this becomes $Ad \ll 0$.

Lemma 4. *Let A be a cooperative matrix. Then A is stable if and only if it is negatively diagonally dominant.*

Proof. First suppose that A is negatively diagonally dominant: There exists a $d \gg 0$ such that $Ad \ll 0$. Note that we must have all $a_{ii} < 0$ since the off-diagonal elements are nonnegative and $d \gg 0$. Let λ be an eigenvalue of A with right eigenvector x. Let $y_i = x_i/d_i$ for $i = 1, \ldots, n$ and $|y_m| = \max_i |y_i| > 0$. Then $\lambda d_i y_i = \sum_{j=1}^{n} a_{ij} d_j y_j$ and

$$\lambda d_m = d_m a_{mm} + \sum_{j\neq m}^{n} d_j a_{mj} \frac{y_j}{y_m}.$$

Therefore

$$|\lambda d_m - d_m a_{mm}| \leq \sum_{j\neq m}^{n} d_j a_{mj} \left|\frac{y_j}{y_m}\right| \leq \sum_{j\neq m}^{n} d_j a_{mj} < -d_m a_{mm}$$

by hypothesis. Hence $|\lambda - a_{mm}| < -a_{mm}$ and λ must lie in the open disc in the Argand plane whose boundary passes through zero and whose centre is at the negative number a_{mm}. Thus all eigenvalues λ have negative real part, so A is stable.

Conversely, suppose that A is stable and has nonnegative off-diagonal elements. For $c > 0$ sufficiently large $B = A + cI$ is a nonnegative matrix and so by the Perron-Frobenius theorem there is a $\lambda = \rho(B) \geq 0$ and a $v > 0$ such that $Bv = \lambda v = \rho(B)v$. But then $Av = (\rho(B) - c)v$ so that, since A is stable, $\rho(B) < c$. Since $\rho(B) < c$ the following series converges

$$A^{-1} = -\frac{1}{c}\left(I + \frac{1}{c}B + \frac{1}{c^2}B^2 + \cdots\right)$$

and thus all elements of A^{-1} are non-positive. Now set $d = -A^{-1}(1,\ldots,1)^T$. Then $d \gg 0$ (no row of A can be zero, since it is nonsingular) and $Ad = -(1,\ldots,1)^T \ll 0$. □

As a corollary we have:

Corollary 1. *If A is cooperative and $r \gg 0$ then $Ax + r = 0$ has a unique interior solution $x \in \mathbb{R}^n_{>0}$ if and only if A is stable.*

Problem 6. *For the system (8) when $c > 0$, $e > 0$ and $\det A > 0$, find the condition for a unique interior steady state.*

We also have the following (see, for example, Theorem 15.1.1 in reference 10):

Theorem 8 (Global convergence for cooperative Lotka-Volterra). *When A cooperative and stable the system (17) has a unique interior steady state that attracts $\mathbb{R}^n_{>0}$.*

Proof. By corollary 1 A is negatively diagonally dominant by lemma 4, i.e there exists a $d \gg 0$ such that $a_{ii}d_i + \sum_{j=1}^n a_{ij}d_j < 0$. Define

$$V(x) = \max_k \frac{|x_k - x_k^*|}{d_k}.$$

Then $V(x) \geq 0$ with equality if and only if $x = x^*$. Now, consider a time interval during which $\max_k \frac{|x_k - x_k^*|}{d_k} = \frac{|x_i - x_i^*|}{d_i}$. Then

$$\begin{aligned}
\dot{V} &= \frac{1}{d_i}\dot{x}_i \mathrm{sgn}(x_i - x_i^*) \\
&= \frac{x_i}{d_i}\left\{a_{ii}(x_i - x_i^*) + \sum_{j\neq i} a_{ij}(x_j - x_j^*)\right\}\mathrm{sgn}(x_i - x_i^*) \\
&\leq \frac{x_i}{d_i}\left\{a_{ii}|x_i - x_i^*| + \sum_{j\neq i} a_{ij}|x_j - x_j^*|\right\} \\
&\leq \frac{x_i}{d_i}V(x)\left\{a_{ii}d_i + \sum_{j\neq i} a_{ij}d_j\right\} \\
&\leq 0 \text{ for all } x \in \mathbb{R}^n_{>0}, \text{ with equality if and only if } x = x^*.
\end{aligned}$$

Hence by Theorem 3, $x(t) \to x^*$ as $t \to \infty$. □

9. Competitive Lotka-Volterra Systems

Now we consider the Lotka-Volterra system

$$\dot{x}_i = x_i(r_i - \sum_{j=1}^{n} a_{ij}x_j) = F_i(x), \quad i = 1, \ldots, n, \tag{18}$$

under the special conditions that $a_{ij} > 0$ for all $1 \leq i, j \leq n$ (**caution:** notice the change of sign in (18)). This means that each species competes with all other species including itself. If some $r_i \leq 0$ then it is clear that $x_i(t) \to 0$ as $t \to \infty$ since $\mathbb{R}^n_{\geq 0}$ is invariant and

$$\dot{x}_i = x_i(r_i - \sum_{j=1}^{n} a_{ij}x_j) \leq -a_{ii}x_i^2 \leq 0,$$

with equality if and only if $x_i = 0$. We will therefore also assume $r_i > 0$ for each $i = 1, \ldots, n$. This means that in the absence of any competitors the species i will evolve according to $\dot{x}_i = x_i(r_i - a_{ii}x_i)$ and hence will either remain at zero or stabilise at its carrying capacity $K_i = r_i/a_{ii} > 0$. It also means that the origin is an unstable node.

Lemma 5. *Since $a_{ij} > 0$ and $r_i > 0$, all orbits of (18) are bounded.*

Proof. $\mathbb{R}^n_{\geq 0}$ is invariant and

$$\dot{x}_i = r_i x_i - x_i \sum_{j=1}^{n} a_{ij}x_j \leq r_i x_i - a_{ii}x_i^2 = x_i(r_i - a_{ii}x_i) < 0 \text{ if } x_i > \frac{r_i}{a_{ii}},$$

so that the ith species is bounded for each $i = 1, \ldots, n$. □

10. Smale's Construction

In the 1970's many thought that for a finite habitat that is home to a number of species that compete with each other and the other species, the long term outcome is "simple" dynamics, e.g. convergence to a steady state or a periodic orbit. But this is not the case, as Stephen Smale showed in 1976.[14] Consider a more general model of **total competition**:

$$\dot{x}_i = x_i M_i(x) = F_i(x), \; (i = 1, \ldots, n), \tag{19}$$

where M_i is smooth and we will suppose that

S1 For <u>all</u> pairs i, j we have $\frac{\partial M_i}{\partial x_j} < 0$ when $x_i > 0$ (totally competitive).
S2 There is a constant K such that for each i, $M_i(x) < 0$ if $|x| > K$.

Condition S1 means that

$$\frac{\partial \dot{x}_i}{\partial x_j} = x_i \frac{\partial M_i}{\partial x_j} < 0 \ \text{ all } i, j \text{ if } x_i > 0. \tag{20}$$

Thus the Jacobian has negative elements in $\mathbb{R}^n_{>0}$. In other words competition for resources. The second condition says that there are finite resources and that the populations can not grow indefinitely.

Smale showed that examples of systems satisfying (19) and the conditions S1, S2 whose long term dynamics lie on a simplex and obey $\dot{x} = h(x)$ on the simplex, where h is any smooth vector field of our choice! Thus the simplex is an attractor upon which arbitrary dynamics can be specified, even chaos.

We follow the presentation of reference 9. Let $\Delta_1 = \{x \in \mathbb{R}^n_{\geq 0} : \|x\|_1 = 1\}$ be the standard probability simplex with tangent space $\Delta_0 = \{x \in \mathbb{R}^n : \sum_{i=1}^n x_i = 0\}$. Let $h_0 : \Delta_1 \to \Delta_0$ be a smooth vector field on Δ_1 whose components can be written as $h_{0i}(x) = x_i g_i(x)$ and $h : \mathbb{R}^n_{\geq 0} \to \Delta_0$ any smooth map which agrees with h_0 on Δ_1.

Now let $\beta : \mathbb{R} \to \mathbb{R}$ be any smooth function which is 1 in a neighbourhood of 1 and $\beta(t) = 0$ if $t \leq \frac{1}{2}$ or $t \geq \frac{3}{2}$. For $\epsilon > 0$ define M_i on $\mathbb{R}^n_{\geq 0}$ by

$$M_i(x) = 1 - \|x\|_1 + \epsilon\beta(\|x\|_1)g_i(x), \ 1 \leq i \leq n.$$

We may check: for each i, j,

$$\frac{\partial M_i}{\partial x_j} = -1 + \epsilon\beta'(\|x\|_1)g_i + \epsilon\beta(\|x\|_1)\frac{\partial g_i}{\partial x_j} < 0,$$

for small enough ϵ since β has compact support.

Now as before, $\mathbb{R}^n_{\geq 0}$ is invariant, and $\frac{d}{dt}\|x\|_1 = \sum_{i=1}^n \dot{x} = \|x\|_1(1 - \|x\|_1)$ (the logistic equation!). Thus Δ_1 is forward invariant and any point in $\mathbb{R}^n_{\geq 0} \setminus \{0\}$ is attracted to Δ_1. On Δ_1 we have

$$M_i(x) = 1 - \|x\|_1 + \epsilon\beta(\|x\|_1)g_i(x) = \epsilon g_i(x),$$

so that the dynamics on the attractor is $\dot{x}_i = x_i\epsilon g_i(x) = \epsilon h_i(x)$ for $i = 1, \ldots, n$, with h arbitrary.

Hence we should be warned that the long term dynamics of bounded competitive systems in dimensions higher than two can be very complex (although one can show [see the next section on the carrying simplex] that when $n = 3$ the long-term dynamics must lie on a set of dimension at most 2, and this severely restricts the possibilities. However, much more is possible when $n \geq 4$.)

11. Carrying Simplices

A bounded totally competitive system with the origin unstable has a unique invariant manifold that attracts the first orthant minus the origin. We will give an example[a] of such a system where the invariant manifold can be explicitly found - it is the probability simplex in $\mathbb{R}^n_{\geq 0}$ - and all orbits save the origin are attracted to it. Moreover, (for that example) the dynamics on the simplex is canonically Hamiltonian and all orbits are periodic.

We consider again the system

$$\dot{x}_i = x_i M_i(x), \ (i = 1, \dots, n),$$

where M_i is smooth and we will suppose that

S1 For all pairs i, j we have $\frac{\partial M_i}{\partial x_j} < 0$.
S2 There is a constant K such that for each i, $M_i(x) < 0$ if $|x| > K$.
S3 $M_i(0) > 0$.

Condition S3 makes the origin 0 a repelling steady state. Since orbits are bounded, the basin of repulsion of 0 in $\mathbb{R}^n_{\geq 0}$ is bounded. The boundary of the basin of repulsion is called the *Carrying Simplex* and is denoted by Σ. One can think of Σ as being the boundary of the set of points whose α limit is the origin.

All steady states and all ω limit sets lie in Σ and we have from Hirsch[8]

Theorem 9 (The Carrying Simplex). *Given (19) every trajectory in $\mathbb{R}^n_{\geq 0} \setminus \{0\}$ is asymptotic to one in Σ, and Σ is a Lipschitz submanifold, everywhere transverse to all strictly positive directions, and homeomorphic to the probability simplex.*

Thus totally competitive $n-$dimensional Lotka-Volterra systems (as above) eventually evolve like $n-1$ dimensional systems. Thus nothing very exotic can happen for $n < 4$. In Figure 3 we display 3 examples of the carrying simplex for totally competitive Lotka-Volterra systems.[1]

The following example has the advantage that the carrying simplex can be found explicitly, and it is easy to see that all points save the origin are attracted to it.

Example 7. We consider the illustrative example of an eventually periodic

[a]A second example, since in Smale's example the unit simplex is also a carrying simplex.

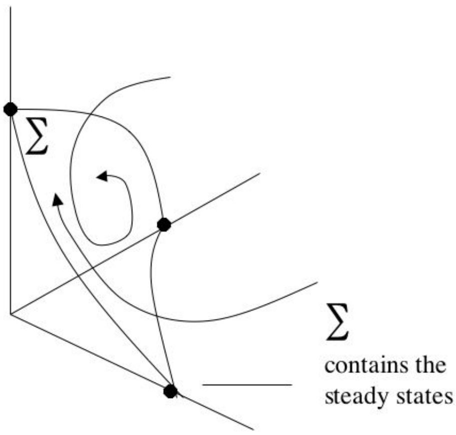

Fig. 2. The Carrying Simplex attracts all orbits except the origin and contains any ω limit set and in particular all steady states except the origin.

competitive system[11]

$$\begin{aligned}\dot{x} &= x(1 - x - \alpha y - \beta z)\\ \dot{y} &= y(1 - \beta x - y - \alpha z)\\ \dot{z} &= z(1 - \alpha x - \beta y - z)\end{aligned}$$

where $\alpha, \beta > 0$ and $\alpha + \beta = 2$. Let

$$V(x, y, z) = xyz.$$

Then

$$\begin{aligned}\frac{d}{dt}V &= xyz\left(\frac{\dot{x}}{x} + \frac{\dot{y}}{y} + \frac{\dot{z}}{z}\right)\\ &= V\left((1 - x - \alpha y - \beta z) + (1 - \beta x - y - \alpha z) + (1 - \alpha x - \beta y - z)\right)\\ &= V(3 - (x + y + z) - (\alpha + \beta)(x + y + z))\\ &= 3V(1 - (x + y + z)) \quad \text{since } \alpha + \beta = 2.\end{aligned}$$

Moreover

$$\begin{aligned}\frac{d}{dt}(x + y + z) &= (x + y + z) - x^2 - y^2 - z^2 - (\alpha + \beta)(xy + xz + yz)\\ &= (x + y + z)(1 - (x + y + z)).\end{aligned}$$

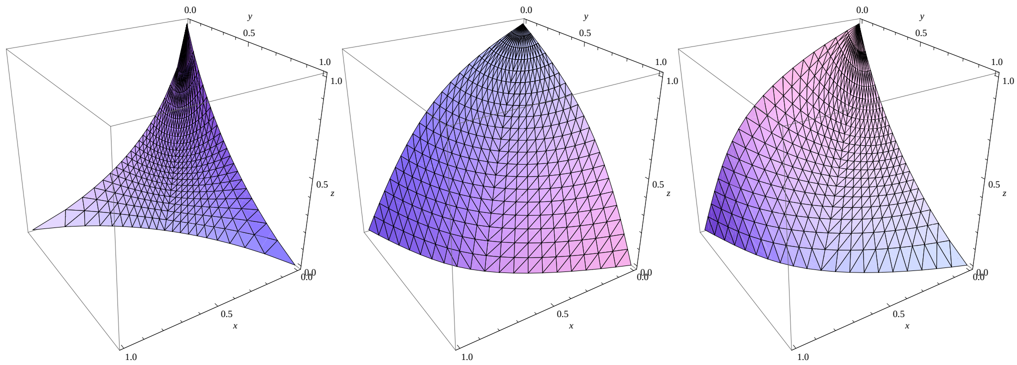

Fig. 3. Examples of the carrying simplex for competitive the 3 dimensional Lotka-Volterra equations. From left to right the carrying simplex is (i) convex, (ii) concave and (iii) saddle-like.[1]

Thus if $(x_0, y_0, z_0) \in \mathbb{R}^3 \setminus (0,0,0)$ we have $x(t)+y(t)+z(t) \to 1$ as $t \to \infty$. That is, all orbits eventually end up on the simplex Δ_1. Thus the carrying simplex Σ in this example is just the simplex Δ_1. On Δ_1 we have

$$\frac{dV}{dt} = 3V(1-(x+y+z)) = 0,$$

that is $V = \text{const}$ on Δ_1. What is the dynamics actually on the carrying simplex? We may eliminate z since $z = 1-x-y$ on the carrying simplex. This gives

$$\begin{aligned} \dot{x} &= x(1-x-\alpha y - \beta(1-x-y)) = \frac{(\alpha-\beta)}{2} x(1-x-2y) \\ \dot{y} &= y(1-\beta x - y - \alpha(1-x-y)) = \frac{-(\alpha-\beta)}{2} y(1-2x-y) \end{aligned}$$

where $\alpha+\beta = 2$. Notice that $\operatorname{div}\,(\dot{x},\dot{y}) = 0$ and that we have a canonical Hamiltonian system with Hamiltonian function

$$H(x,y) = \frac{(\alpha-\beta)}{2}(1-x-y)xy.$$

On the open triangle $T = \{(x,y) \in \mathbb{R}^2_{\geq 0} : 0 < x+y < 1\}$ we obtain closed contours, i.e. the solutions are periodic. (This is the projection of the dynamics on Σ onto the $xy-$plane.) Figure 7 shows the periodic orbits on the invariant plane $\Sigma = \{x \in \mathbb{R}^3_{\geq 0} : x_1+x_2+x_3 = 1\}$ as part of the 3-dimnesional phase portrait.

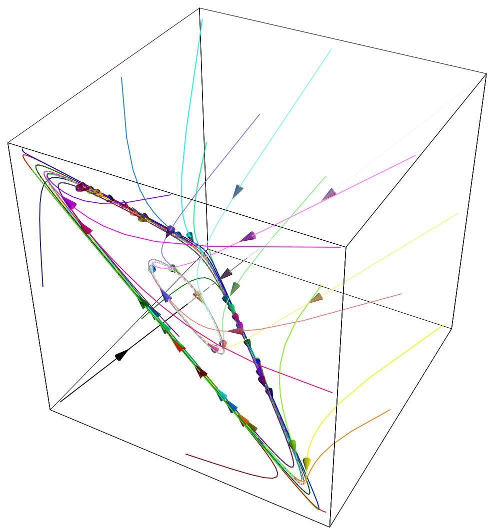

Fig. 4. Periodic orbits in a model of May and Leonard.[11] Note the carrying simplex is the usual simplex in $\mathbb{R}^3_{\geq 0}$ and it clearly attracts all orbits apart from the origin.

Problem 7. *Consider the planar competitive system*[20]

$$\dot{x} = x(1 - x - \frac{y}{2})$$
$$\dot{y} = y(1 - 3x - y).$$

Show that this system has a carrying simplex Σ which is the graph of a quadratic function q that satisfies $q(0) = 1$ and $q(1) = 0$. Sketch the phase plane.

12. Further reading

The book by Takeuchi (reference 16) provides a comprehensive study of Lotka-Volterra equations. Hofbauer and Sigmund[10] contains much on Lotka-Volterra systems, plus also their close cousins the Replicator equations from evolutionary game theory. The cooperative and competitive Lotka-Volterra models discussed here are a small subset of monotone dynamical systems which are covered in reference 9 by Hirsch and Smith. See also the monograph on monotone dynamical systems by Smith.[15] In 2003 a new geometrical approach to the study of Lotka-Volterra systems was initiated by M. L. Zeeman and E. C. Zeeman.[19] The carrying simplex of competition models originated in a 1988 paper by Hirsch.[8] The geometry of carrying simplices has been studied by Tineo[17] and more recently by Baigent,[1] where in the latter paper links are made to the geometrical approach of Zeeman and Zeeman.[19]

13. Sketch solutions to problems

Problem 1:

$$\dot{x} = x(1 - x - y) \tag{21}$$

$$\dot{y} = y(-1 - y + x). \tag{22}$$

From (21) we see that for any initial condition, since $y(t) \geq 0$, for t large enough $0 \leq x(t) \leq 1$. But then, from (22) eventually $\dot{y} < 0$ and so we must have $y(t) \to 0$ as $t \to \infty$. It is thus clear that all orbits are bounded and each $\omega((x_0, y_0))$ is nonempty. If $(p_1, p_2) \in \omega((x_0, y_0))$, then for some $t_k \to \infty$, $p_2 = \lim_{k\to\infty} y(t_k) = 0$. Thus $\omega((x_0, y_0)) \subset \{(s, 0) : s \in [0, 1]\}$. If $(P_1(t), 0)$ is the forward orbit with $(P_1(0), 0) = (p_1, 0) \in \omega((x_0, y_0))$ and $p_1 > 0$ then by invariance $(P_1(t), 0) \in \omega((x_0, y_0))$ for all $t \in \mathbb{R}$. But $P_1(t)$ satisfies $\dot{P}_1 = P_1(1 - P_1)$ and so $p_1 = \lim_{k\to\infty} P_1(t_k) = 1$. Hence for any $(x_0, y_0) \in \mathbb{R}^2_{\geq 0} \setminus \{(0, 0)\}$ we have $\omega((x_0, y_0)) = \{(1, 0)\}$, and $\omega((0, 0)) = \{(0, 0)\}$.

Problem 2

The system $\dot{x} = x(1 - x)$ has invariant sets $\{0\}$, $\{1\}$, $[0, 1]$, $\{0, 1\}$, $\mathbb{R}_{\geq 0}$, $\mathbb{R}_{\geq 0} \setminus \{1\}$. The forward invariant sets are $[s_1, s_2]$ for any $0 \leq s_1 \leq 1 \leq s_2$. $B(1) = \mathbb{R}_{>0}$.

Problem 3

No, the converse does not hold. Take the system $\dot{x} = x(1 - \frac{x}{2} - \frac{y}{2})$ and $\dot{y} = y(-1 + x + \frac{y}{8})$. Then there is a steady state $(\frac{6}{7}, \frac{8}{7})$ which globally attracts $\mathbb{R}^2_{>0}$, with $\det A = \frac{7}{16} > 0$ and $b = -\frac{1}{2} < 0$ but $f = \frac{1}{8} > 0$.

Problem 4

Set $x = \log N, y = \log P$. Then $\dot{x} = a - be^y, \dot{y} = ce^x - d$. Set $H(x, y) = ay + dx - ce^x - be^y$. Then $\frac{\partial H}{\partial x} = d - ce^x = -\dot{y}$ and $\frac{\partial H}{\partial y} = a - be^y = \dot{x}$. Then $\dot{H} = \frac{\partial H}{\partial x}\dot{x} + \frac{\partial H}{\partial y}\dot{y} = 0$, so that H is constant along orbits.

Problem 5

$\{f, g\} = \nabla f \cdot A\nabla g$, where $A^T = -A$. Then using the summation convention $\{g, h\} = a_{ij}\frac{\partial g}{\partial x_i}\frac{\partial h}{\partial x_j}$. Thus $\{f, \{g, h\}\} = a_{ij}\frac{\partial f}{\partial x_i}\frac{\partial}{\partial x_j}\left(a_{lk}\frac{\partial g}{\partial x_l}\frac{\partial h}{\partial x_k}\right) = a_{ij}a_{lk}\frac{\partial f}{\partial x_i}\left(\frac{\partial^2 g}{\partial x_l \partial x_j}\frac{\partial h}{\partial x_k} + \frac{\partial g}{\partial x_l}\frac{\partial^2 h}{\partial x_k \partial x_j}\right) = a_{ij}a_{lk}\left(\frac{\partial f}{\partial x_i}\frac{\partial h}{\partial x_k}\frac{\partial^2 g}{\partial x_l \partial x_j} + \frac{\partial f}{\partial x_i}\frac{\partial g}{\partial x_l}\frac{\partial^2 h}{\partial x_k \partial x_j}\right)$. By cycling terms $\{g, \{h, f\}\} = a_{ij}a_{lk}\left(\frac{\partial g}{\partial x_i}\frac{\partial f}{\partial x_k}\frac{\partial^2 h}{\partial x_l \partial x_j} + \frac{\partial g}{\partial x_i}\frac{\partial h}{\partial x_l}\frac{\partial^2 f}{\partial x_k \partial x_j}\right)$

and $\{h,\{f,g\}\} = a_{ij}a_{lk}\left(\frac{\partial h}{\partial x_i}\frac{\partial g}{\partial x_k}\frac{\partial^2 f}{\partial x_l \partial x_j} + \frac{\partial h}{\partial x_i}\frac{\partial f}{\partial x_l}\frac{\partial^2 g}{\partial x_k \partial x_j}\right)$. Consider second derivatives of h the sum $\{f,\{g,h\}\} + \{g,\{h,f\}\} + \{h,\{f,g\}\}$; this gives $a_{ij}a_{lk}\frac{\partial f}{\partial x_i}\frac{\partial g}{\partial x_l}\frac{\partial^2 h}{\partial x_k \partial x_j} + a_{ij}a_{lk}\frac{\partial g}{\partial x_i}\frac{\partial f}{\partial x_k}\frac{\partial^2 h}{\partial x_l \partial x_j} = a_{ij}a_{lk}\frac{\partial f}{\partial x_i}\frac{\partial g}{\partial x_l}\frac{\partial^2 h}{\partial x_k \partial x_j} - a_{ij}a_{lk}\frac{\partial g}{\partial x_i}\frac{\partial f}{\partial x_l}\frac{\partial^2 h}{\partial x_k \partial x_j} = a_{ij}a_{lk}\frac{\partial^2 h}{\partial x_k \partial x_j}\left(\frac{\partial g}{\partial x_i}\frac{\partial f}{\partial x_l} - \frac{\partial f}{\partial x_i}\frac{\partial g}{\partial x_l}\right)$. This value of this last expression is not changed by interchanging labels i, l, whereas the bracketed term changes sign, and so the expression must be zero.

Problem 6

The conditions are $\det A = bf - ec > 0$ and $dc > fa, ea > db$. Since $ec > 0$ we must have $bf > 0$, and hence either (i) $b, f > 0$ or (ii) $b, f, < 0$. If $b, f > 0$ then $\frac{c}{f}d > a$ and $\frac{e}{b}a > d$. From these it is clear that both cannot be satisfied unless $a, d > 0$. If $b, f > 0$ and $a, d > 0$ then the condition is $\frac{b}{e} < \frac{a}{d} < \frac{c}{f}$. (Of course, even if an interior steady state exists, the cooperative system $(e, c > 0)$ may have unbounded orbits).

Problem 7

An invariant curve connecting $(1,0)$ and $(0,1)$ is a solution $y : [0,1] \to \mathbb{R}_{\geq 0}$ of $y'(x) = \frac{y(1-3x-y)}{x(1-x-\frac{y}{2})}$ that satisfies the boundary conditions $y(0) = 1$ and $y(1) = 0$. Let the quadratic be $y(x) = 1 + ax + bx^2$. Then this satisfies the boundary condition $y(0) = 1$. To satisfy $y(1) = 0$ we need $0 = 1 + a + b$ so that we need $a = -1 - b$, and y takes the form $y(x) = 1 - (1+b)x + bx^2 = (1-x)(1-bx)$. For this function $y'(x) = -1 - b + 2bx$, so that $y'(0) = -1 - b$. On the other hand $y'(x) = \frac{y(1-3x-y)}{x(1-x-\frac{y}{2})}$, so by L'Hôpital's rule $y'(0) = \frac{y(0)\left(-y'(0)-3\right)+(1-y(0))y'(0)}{1-\frac{y(0)}{2}}$. Now set $y(0) = 1$ to obtain $y'(0) = -2$, which implies $b = 1$, and thus that the curve is $y(x) = (1-x)^2$. It is now simple to check that $y(x) = (1-x)^2$ satisfies $y'(x) = \frac{y(1-3x-y)}{x(1-x-\frac{y}{2})}$ and so the graph of y is an invariant manifold. See Figure 5 for the phase portrait.

References

1. S. Baigent. Geometry of carrying simplices of 3-species competitive Lotka-Volterra systems. *Nonlinearity*, 26(4), 1001–1029 (2013).
2. N. P. Bhatia and G. P. Szegö. Stability theory of dynamical systems (Vol. 161). Springer Science & Business Media. 2002.
3. A. Berman and R. J. Plemmons. Nonnegative matrices in the Mathematical Sciences. Classics in Applied Mathematics (Vol. 9). SIAM, 1994.
4. C. Carmen. Ordinary differential equations with applications. Texts in Applied Mathematics Vol 34. Springer-Verlag. 2006.
5. P. Duarte, R. L. Fernandes, W. M. Olivia. Dynamics on the attractor of the

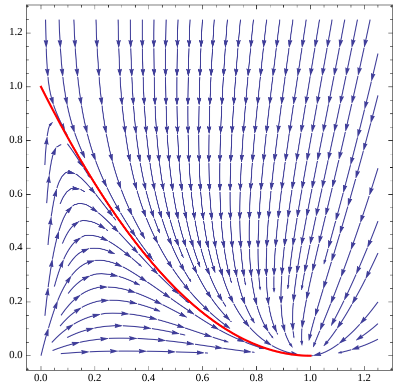

Fig. 5. Problem 7. There is a carrying simplex Γ that connects the two axial steady states $(1, 0)$ and $(0, 1)$. Γ is the graph of the function $y(x) = (1 - x)^2$ over $[0, 1]$ and attracts all points except the origin, which is a steady state.

Lotka-Volterra equations. *J. Diff Eqns* 149, 143–189 (1998).

6. B. S. Goh. Global Stability in Two Species Interactions. *J. Math Biol.*, 3, 313–318 (1976).
7. B. S. Goh. Stability in Models of Mutualism. *The American Naturalist*, 113, No. 2, 261–275 (1979).
8. M. W. Hirsch. Systems of differential equations which are competitive or cooperative: III. Competing species. *Nonlinearity*, 1, 51–71 (1988).
9. M. W. Hirsch and H. L. Smith. Monotone Dynamical Systems. In Handbook of Differential Equations, Ordinary Differential Equations (second volume). Elsevier, Amsterdam. 2005.
10. J. Hofbauer and K. Sigmund. Evolutionary Games and Population Dynamics. CUP. 2002.
11. R. W. May and W. J. Leonard. Nonlinear aspects of competition between three species. *SIAM J. Applied Math*, 29, 243–253 (1975).
12. J. E. Marsden and T. Ratiu. Introduction to Mechanics and Symmetry. Texts in Applied Mathematics Vol 17. Springer-Verlag. 1994.
13. L. Perko. Differential Equations and Dynamical Systems (Third Edition). Texts in Applied Mathematics 7. Springer. 2001.
14. S. Smale. On the Differential Equations of Species in Competition. *J. Math Biol.*, 3, 5–7 (1976).
15. H. L. Smith. Monotone Dynamical Systems. AMS, Providence, R.I. 1995.
16. Y. Takeuchi. Global dynamical properties of Lotka-Volterra systems. Singapore: World Scientific. 1996.
17. A. Tineo. On the convexity of the carrying simplex of planar Lotka-Volterra competitive systems. *Applied Mathematics and Computation*, 1–16. (2001).
18. V. Volterra. Leçons sur la Théoerie Mathématique de la Lutte pour la Vie. Gauthier-Villars et Cie., Paris. 1931.

19. M. L. Zeeman and E. C. Zeeman. From local to global behavior in competitive Lotka-Volterra systems. *Trans. Amer. Math. Soc.*, 355:713–734. (2003).
20. E. C. Zeeman. Classification of quadratic carrying simplices in two-dimensional competitive Lotka-Volterra systems. *Nonlinearity*, 15(6), 1993–2018, (2002).